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SEXUALITY IN RHIZINA UNDULATA FRIES

HARRY MORTON FITZPATRICK

(WITH PLATES III AND IV)

Although in recent years a considerable number of papers have appeared dealing with the phenomena of sexuality in the Ascomycetes, certain of the natural orders in this group have received little attention. In the Discomycetes practically all the species which have been investigated are members of the Pezizales, and few facts are available concerning the sexual process in representatives of any other order. Our knowledge of the morphology of the sexual organs and the behavior of the sex nuclei in the Helvellales is particularly meager. The following brief discussion of the important papers which have been published on the cytology of these fungi will serve to emphasize this fact.

BROWN (11) describes the development of the ascocarp in two species of *Leotia*. In *L. lubrica*, at the base of the youngest fruit-body sectioned, he discovered a large, vacuolated cell having the appearance of an emptied ascogonium. From this cell he found arising a number of hyphae of larger diameter than the other hyphae of the ascocarp. These larger hyphae were empty, and, although they could not be followed for any great distance, they seemed to be connected higher in the fruit-body with the ascogenous hyphae. He apparently found evidences of this ascogonium-like structure in only one specimen, since he states nothing to the contrary, and does not describe other stages in its development. He gives no data

concerning nuclear conditions in this cell nor in the hyphae to which it gives rise, and makes no mention either of the presence or absence of an antheridium. Moreover, in the single other species which he studied, *L. chlorocephala*, he finds no indication of the presence of sexual organs, and states merely that the ascogenous hyphae have their origin in the stipe.

CARRUTHERS (**14**) discusses in some detail the cytology of *Helvella crispa*, placing particular emphasis on the nuclear divisions in the ascus. He states definitely that sexual organs are absent in this species, and describes apogamous nuclear fusions in undifferentiated hyphae of the hypothecium. Although in the summary of his paper he states that the cells containing the fusion nuclei give rise to the ascogenous hyphae, this important point is not mentioned in the discussion of his results and no figures are given demonstrating it. He states further that "there is evidence that mitoses in the vegetative and ascogenous hyphae show respectively 2 and 4 chromosomes," and says that the third nuclear division in the ascus is brachymeiotic, there being 4 chromosomes in the prophase, while only 2 pass to the poles.

DITTRICH (**24**) states that in *Mitrula phalloides* the ascogenous hyphae arise near the center of the fruit-body from a complex of closely massed, elongated, deeply staining filaments characterized by the possession of large nuclei with prominent nucleoli. He finds no sexual organs, and does not describe an approximation or fusion of nuclei in the hypothecium.

MCCUBBIN (**53**) states that in *Helvella elastica* "no structure having the conventional form of an ascogonium" is found, and says that the ascogenous hyphae "arise as a clearly differentiated subhymenial complex of filaments." However, he describes at considerable length large cellular bodies which occur irregularly throughout the whole of the ascocarp except the stem. He regards these as vegetative in function and calls them storage bodies. In the earliest stages in the development of the fruit-body they are absent, but they appear relatively early. They are large, attaining in some cases 20–30 times the diameter of the surrounding hyphae, are filled with deeply staining protoplasm, and exhibit remarkable variation in shape. They sometimes form a chain

of 3 or 4 connected cells. By the time the asci are mature they are usually empty, their connections have disappeared, and their walls have collapsed. McCUBBIN states that these structures in some instances give rise to palisade hyphae and paraphyses, while at other times they are found "having the ascogenous hyphae proceeding directly from them." They contain nuclei varying in number from 1 to 20 or more, a conspicuous feature being the frequent arrangement of these nuclei in pairs. McCUBBIN gives a number of illustrations showing the variation in size and shape of these structures and demonstrating clearly the paired condition of the nuclei. Several significant facts would seem to indicate that at least part of these "storage bodies" constitute some type of sexual apparatus, particularly the statement that they are sometimes found giving rise to the ascogenous hyphae.

FAULL (**26**) discusses the method of origin of the asci from the ascogenous hyphae in a considerable number of species representative of various genera of the Helvellales. He has not investigated the sexual process, however, or described sexual organs in any of the forms studied.

In so far as the writer is aware, no other papers of importance bearing on the sexual process in the Helvellales have appeared. In no member of this group is our knowledge more than fragmentary; in fact it cannot be stated with certainty that any worker has seen the sexual organs in any species of the order. The family Rhizinaceae has received no attention whatever from the standpoint of cytology. As representative of this family, *Rhizina undulata* Fries, is especially suitable for investigation. It is the type of the genus and the family, and probably the most widely distributed and best known member of the group.

Materials and methods

In the summer of 1914 the writer collected a considerable number of apothecia of *Rhizina undulata* in a small pine wood north of Beebe Lake near the Cornell University Campus at Ithaca, New York. Fruit-bodies of practically all stages of development were obtained. The youngest stages, including undifferentiated primordia, were studied, and the results of the investigation were

embodied in an account of the origin of the ascocarp in this species (FITZPATRICK **27**). During the course of this investigation the examination of certain slides disclosed the fact that the material was favorable for a study of the sexual process. Additional slides were then prepared, and material of all ages was given critical examination.

The apothecia were fixed in the field in medium strength chromo-acetic acid fixer, and were later imbedded in paraffin. The material was studied in serial sections 4–7 μ in thickness and was stained in most cases with Haidenhain's iron alum-haematoxylin, although for certain stages the shortened Flemming's triple stain proved more satisfactory.

Certain of the apothecia on which the investigation is based were sectioned and stained in the laboratories of the Brooklyn Botanic Garden in the summer of 1915, while the writer held a visiting fellowship at that institution. He wishes to express here his appreciation of the courtesy of Director C. S. GAGER in extending to him all the facilities of the laboratories and gardens, and to acknowledge his indebtedness to Dr. E. W. OLIVE for many kindnesses, including helpful suggestions concerning microtechnique. Subsequently other apothecia were sectioned and stained in the laboratories of the Department of Plant Pathology at Cornell University. All the critical study of the material was made at the latter institution during the spring of 1916. The writer's identification of the species as *Rhizina undulata* was confirmed independently by Dr. E. J. DURAND and Dr. F. J. SEAVER. The completed manuscript was examined by Professor GEORGE F. ATKINSON. His criticisms, especially with reference to the interpretation of the meaning of the paired condition of the nuclei in the cells of the archicarp, have been embodied in the text, and have resulted in extensive alterations. The writer wishes to express his appreciation of these favors.

Vegetative hyphae

The mycelium of *Rhizina undulata* is parasitic on the roots of various trees (HARTIG **42, 43, 44,** TUBEUF **63,** WEIR **64**). It develops profusely in the soil also, enveloping the soil particles and smaller roots as a whitish, moldlike growth. On the surface of the ground

and on partially exposed roots a definite subiculum is thus produced, upon which minute, snow white knobs of mycelium are developed. These constitute primordia of fruit-bodies. They are composed of undifferentiated hyphae, but a somewhat indefinite palisade layer is formed over the periphery of the primordium. At their initiation, these primordia are extremely minute, averaging approximately 0.3 mm. in lateral diameter. There is no indication other than shape that they are to develop into ascocarps. Sexual cells at this early period are certainly absent. The hyphae composing the primordium are all of approximately the same diameter, and consist of narrow, cylindrical, multinucleate cells. Uninucleate or binucleate cells are not found. These hyphae in many instances can be traced back toward the point of origin of the primordium, where they are either lost in the tangle of hyphae composing the subiculum or are found to enter the soil.

The ascocarp primordium increases in size chiefly by the elongation and branching of the palisade hyphae at the periphery. At the same time the palisade layer becomes more sharply demarcated. The fruit-body, as demonstrated by the writer in his earlier paper, is not, either at the beginning or at any later period, provided with an enveloping membrane. The ascocarp in this species is therefore gymnocarpous, the hymenium being "exposed from the first."

The nuclei in the cells of the vegetative hyphae are small, and were studied with difficulty. A small amount of chromatic material and a deeply staining nucleolus may be seen in each. No division figures have been observed. It is possible that mitosis occurs only at night, all the material having been placed in the fixer at one time during the day. However, the minute size of the nuclei would render any study of nuclear division in the vegetative hyphae extremely difficult. The nuclei occur irregularly throughout the hyphae, and give no indication of pairing or of any other definite arrangement. Deeply staining granules are present in the cytoplasm. These extranuclear bodies, possibly the metachromatic granules of GUILLIERMOND (**35**), are of doubtful function. Sometimes they are found grouped over the opposite faces of the transverse septa. A similar condition exists in *Ascophanus carneus*, where, according to CUTTING (**18**), they guard a minute pore in the

septum. In *R. undulata* no such pores have been demonstrated. Such protoplasmic connections, however, are of frequent occurrence in the fungi. They were first observed by CHMIELEWSKY (**15**). Subsequently they have been the object of research by DANGEARD (**19, 20, 21**) in *Sphaerotheca Humuli*, *Bactridium flavum*, and other fungi; and have been studied in various species by MASSEE (**52**), KIENITZ-GERLOFF (**48**), MEYER (**54**), GUILLIERMOND (**37**), and others. MEYER in particular has given them considerable attention and has demonstrated that open pores exist in the transverse septa of the hyphae of many Basidiomycetes and Ascomycetes. They possibly function in permitting a more rapid transfer of food material from cell to cell.

Archicarp

When the ascocarp primordium has attained a diameter of approximately 1 mm., differentiation begins to take place, certain hyphae lying near its center undergoing transformation into archicarps. The number of archicarps developed in the interior of a single ascocarp varies, and when several archicarps lie closely approximated their interweaving renders an exact count difficult. A careful study, however, of all the consecutive sections of a complete series through the ascocarp demonstrates that the number is in some cases as many as 8, and in many individuals probably more. No ascocarp containing less than 3 archicarps has been found. Although lateral fusion of adjacent apothecia resulting in the formation of irregular compound structures is a common phenomenon, it fails to explain the presence of more than a single archicarp in a fruit-body. Ascocarps of circular form which are clearly the result of the enlargement of a single primordium contain several archicarps. Moreover, young primordia in which lateral fusions have certainly not taken place reveal several archicarps in the process of development.

While the production of several archicarps in a single apothecium is unusual in the Discomycetes, this condition being more typical of the discomycetous lichens, it is not unique. OVERTON (**56**) finds that in *Thecotheus Pelletieri* the apothecium is compound, the fruit-body arising from several multicellular archicarps. In other Discomycetes, of which *Pyronema confluens* is perhaps the

best known example, several pairs of ascogonia and antheridia contribute to the formation of a single apothecium. In the majority of the Discomycetes which have been studied, however, a single archicarp is developed. Of these may be enumerated *Lachnea scutellata* (BROWN **12**, WORONIN **69**), *Peziza granulosa* and *Ascobolus pulcherrimus* (WORONIN **69**), *Ascobolus furfuraceus* (JANCZEWSKI **45, 46**, HARPER **39**, WELSFORD **65**), *Ascodesmis nigricans* (VAN TIEGHEM **61**), *Ryparobius* sp. (BARKER **4, 5**), *Thelebolus stercoreus* (RAMLOW **57**), *Lachnea scutellata* (BROWN **12**), *Humaria granulata* (BLACKMAN and FRASER **9**), *Ascophanus carneus* (CUTTING **18**), and *Lachnea cretea* (FRASER **30**). As representative of lichens containing several archicarps in a single apothecium may be listed *Parmelia acetabulum* (BAUR **7, 8**), *Anaptychia ciliaris*, *Lecanora subfusca*, *Endocarpon miniatum*, *Gyrophora cylindrica*, and *Cladonia pyxidata* (BAUR **8**), *Pertusaria communis* and *Pyrenula nitida* (BAUR **7**), and several species of *Collema* (BAUR **6**, BACHMANN **2, 3**).

The individual archicarp of *R. undulata* arises by the rapid growth and transformation of a single multicellular hypha. The cells increase greatly in lateral diameter and become filled with deeply staining protoplasm, so that the resulting structure assumes a dense and opaque appearance. The relatively few nuclei originally present undergo repeated division, and each cell of the archicarp is soon packed with many nuclei. The cells of the archicarp are certainly multinucleate from the first. In *Ascobolus*, according to HARPER (**39**) and WELSFORD (**65**), the cells of the archicarp are uninucleate at the beginning, while in other forms (BROWN **12** *Lachnea scutellata*, CUTTING **18** *Ascophanus carneus*) they are described as multinucleate in all stages.

The diameter of the cells of the archicarp when the ultimate size is reached is much greater than that of the surrounding hyphae, and for this reason no possibility exists of mistaking an archicarp for an ordinary hypha, even when the lower powers of the microscope are used. This difference in size is strikingly shown in fig. 4. Cells of a mature archicarp sometimes measure 10 times the diameter of the other hyphae.

The archicarp is in all cases multicellular, the number of cells varying in the counts made from 10 to 19. Different individuals

have been followed carefully from base to apex throughout the various sections of a series, and the cells are found to differ to a marked degree in size and shape. Great variability is also shown in the general form of the archicarp (figs. 1–4). It develops in some cases as a loose coil (fig. 3), in others winds irregularly among the other hyphae (fig. 1), or more rarely bends back upon itself, forming two nearly parallel rows of cells (fig. 4). Irregularly winding archicarps are the most common type. Closely wound coils have not been found. Antheridia are not produced, and no fusion of the terminal cell of the archicarp with any other structure has been observed. Many sections have been examined in vain in an endeavor to demonstrate such fusions. The writer is convinced that none occur.

The terminal cell of the archicarp is smaller than the other cells of this structure. It is usually narrow and attenuated, and at the maturity of the archicarp shows disorganized, deeply staining, protoplasmic contents. It resembles very closely the cell figured and described by CUTTING (**18**) as a trichogyne in *Ascophanus carneus*, and from analogy the writer will refer to it as the trichogyne. It certainly does not function, however, and is evidently merely a vestigial structure.

The archicarp in *R. undulata* is not, as in certain other species, sharply divided into definite apical, central, and basal portions. The cells which give rise to ascogenous hyphae are usually centrally located in the coil, and in some individuals are slightly larger than the other cells, but this is not always the case. No well defined ascogonium is differentiated.

In the younger stages in the development of the archicarp no pores can be detected in the transverse septa. If any exist, they are very minute. Deeply staining, extranuclear granules, resembling those in the vegetative hyphae, are frequently found grouped on opposite sides of the cross walls. Their occurrence is not constant and their function is unknown. Similar granules are also described as occurring in *Ascobolus* (HARPER **39**, WELSFORD **65**), *Ascophanus carneus* (CUTTING **18**), *Pyronema confluens* (HARPER **40**), *Humaria granulata* (BLACKMAN and FRASER **9**), and other Ascomycetes.

As the archicarp of *R. undulata* approaches maturity a very prominent, deeply staining, hemispherical or convex pad appears on each side of each cross wall at or near its center. Similar pads have been found in *Humaria granulata* (BLACKMAN and FRASER **9**), *Ascophanus carneus* (CUTTING **18**), and other forms, but in no case have the figures presented by the investigator shown such striking and definite structures as those in *R. undulata*. Since at a somewhat later period a single large pore appears in each of the transverse septa at the point earlier occupied by the pads, it seems probable that the latter represent a swelling out of the septum due to gelatinization at this point. CUTTING has suggested that the metachromatic granules mentioned may function in bringing about such a gelatinization. It is certain, in any case, that the pads are absent in young archicarps; that with the approach of maturity they are prominent; and that still later they disappear, leaving behind a well defined pore in the septum. CUTTING found pads in *Ascophanus carneus* lying free in the cytoplasm of the archicarp following the appearance of the pores. Attached to these he observed what seemed to be bits of the wall on which they originally lay. The writer, however, has not seen any such detached pads in *R. undulata*.

Near the apex of the archicarp shown in fig. 3 may be seen the union of the two pads which originally lay separated on the opposite faces of the septum. We may assume that this fusion represents the last stage in gelatinization. CUTTING (**18**) figures a similar condition (his fig. 14) in an archicarp of *Ascophanus carneus*.

Although the disappearance of these pads takes place suddenly, the process does not occur simultaneously on all the transverse septa. In fact, neither in the development of the pads nor in their removal is any definite sequence followed as regards the relative position of the septa in the archicarp. In the youngest archicarp shown (fig. 1) not all of the pads have been formed. In an older archicarp (fig. 4) all have disappeared, leaving definite open protoplasmic connections. In intermediate stages (figs. 2, 3) some pads have disappeared while others remain.[1] Rarely a single pair of pads persists on a septum until the formation of ascogenous hyphae has

[1] Read the introductory paragraph in the explanation of plates.

progressed to a marked degree (fig. 7). The mature archicarp, on account of its very dense protoplasmic contents and numerous nuclei, stains very deeply, and in many cases is practically opaque. Not all the individuals stained prove favorable, therefore, for the demonstration of protoplasmic continuity. Moreover, on account of the winding course of the archicarp, which results in the appearance of different portions of a single coil in several different sections, not all of the pores or pads are visible in the plane of one section. When the position of the archicarp is favorable careful staining renders the pores very evident (figs. 4, 7). They are slightly greater in diameter than a single nucleus. The ascogenous hyphae in some cases (figs. 3, 7) arise before all of the pads have disappeared; in other cases (fig. 4) all of the pores may be formed before any indication of the development of ascogenous hyphae is given.

Ascogenous hyphae

As stated earlier, no definite group of cells in the archicarp gives rise to the ascogenous hyphae. Usually 4 or 5 consecutive cells lying near the center of the coil function as ascogonial cells. These put out a considerable number of ascogenous hyphae, which by repeated branching develop a large number of free ends for the formation of ascus hooks. The other cells of the archicarp meantime fail to bud, and their nuclei and cytoplasm flow through the open connections in the transverse septa into the active ascogonial cells and thence into the ascogenous hyphae. All the cells of both the apical (exclusive of the trichogyne) and basal regions contribute their contents to this general flow, and are finally almost entirely emptied. This migration is shown clearly in figs. 5 and 6. Figs. 8, 9, 10, and 11 represent at a considerably higher magnification sections through ascogonial cells at right angles to the long axis of the archicarp. In two of these (figs. 10, 11) the ascogenous hyphae are shown at their point of origin from the archicarp. The others (figs. 8, 9) represent sections through budding cells at points between the places where hyphae arise. A pronounced vacuolation of the cytoplasm of the ascogonial cells occurs at the time of the outward flow of nuclei into the ascogenous hyphae. Since the vacuolation is more evident in the center of the cell, the nuclei

which remain behind lie at this stage in a rather restricted zone at the periphery.

This pronounced vacuolation and thinning of the cytoplasm of the ascogonial cells renders less difficult the study of the nuclei, and at this stage, in the writer's preparations, they seem always to lie in pairs. At no other stage in the development of the archicarp, either before or after the formation of pores in the transverse septa, have paired nuclei been found in any of the cells of this structure. This, however, may be due in large measure to the fact that the dense nature of the cytoplasm and the crowding of the nuclei render the determination of this point extremely difficult.

The presence of paired nuclei in any of the cells of the archicarp is a matter of the greatest interest and importance. This is especially true since an antheridium is absent. The determination of the origin of the two nuclei which constitute a pair, however, is fraught with considerable difficulty. It is evident that they are either potential sex nuclei which have had their respective origins in the same or different cells of the archicarp, or sister nuclei which have resulted from a recent more or less simultaneous division of the archicarp nuclei. If they are sex nuclei, it is to be expected that they will either fuse in the archicarp or migrate side by side into the ascogenous hyphae, where they will undergo conjugate divisions preceding the fusion in the ascus.

Fusion of these pairs of nuclei in the cells of the archicarp has not been observed. Although occasionally the two nuclei lie in actual contact, fusion stages have not been found. Moreover, no nuclei of larger size have been seen which might from analogy be assumed to be fusion nuclei. A thorough examination of the nuclei in the ascogenous hyphae has failed, moreover, to demonstrate conjugate divisions. In some instances groups of nuclei in fours have been found lying in such a position as to suggest their origin from conjugate divisions, but these cases are not numerous enough to carry conviction. No mitotic figures, either of simple or conjugate division, have been seen in these hyphae, nor in any of the cells of the archicarp. The writer has attributed their absence to the fact that all of his material was placed in the fixing solution at one time. Periodicity of mitosis thus could easily explain their

absence in all of the preparations. Since *R. undulata* is an uncommon species, it is infrequently collected, and the writer, desirous of supplementing his material with preparations showing mitosis, searched for the fungus without success throughout the summers of 1915 and 1916. While unwilling to state that conjugate divisions do not take place in the ascogenous hyphae of this species, he has been unable to demonstrate their occurrence. On the other hand, a periodicity in mitosis which would constitute a more or less simultaneous division of all the nuclei in the archicarp might easily give at the rounding up of the daughter nuclei a marked appearance of pairing. The pairs of nuclei in the ascogenous hyphae could also originate in the same manner. Until mitotic figures, either of simple or conjugate divisions, have been demonstrated in the ascogenous hyphae, it will be well to reserve judgment as to the meaning of the paired condition.

A comparison of our work on *R. undulata* with that of other investigators who have studied the origin of the paired condition in those Ascomycetes in which a male organ is lacking or nonfunctional is not enlightening. Although great variation exists in their accounts, fusion of nuclei in pairs in the ascogonial cells is described as occurring in *Lachnea cretea* (FRASER **30**), *Ascophanus carneus* (CUTTING **18**), and *Thecotheus Pelletieri* (OVERTON **56**). Conjugate divisions have not been described in any case. CLAUSSEN (**17**) alone in *Pyronema confluens* has figured conjugate divisions in the undifferentiated portions of the ascogenous hyphae of the Discomycetes.

The ascogenous hyphae of *R. undulata* undergo repeated branching as they approach the hymenium. They soon become multiseptate (fig. 12), the individual cells containing a varying number of nuclei which are usually, though not constantly, in evident pairs. On the transverse septa are found deeply staining granules resembling those in the vegetative hyphae. In some cases these are aggregated into large granules similar to the deeply staining pads of the archicarp, but they are in reality much smaller. Other granules occur throughout the cytoplasm. No open pores in the septa have been demonstrated, and although it is possible that minute protoplasmic connections exist, there is no reason to think that nuclei migrate from cell to cell. In later stages the deeper lying

cells of the ascogenous hyphae become vacuolated, stain lightly, and apparently take no direct part in the formation of the hymenium.

The layer of paraphyses is developed early in the history of the fruit-body and constitutes a well defined zone long before the young asci are developed. This zone is in reality merely a differentiation of the palisade layer of peripheral vegetative hyphae, and its elements have no direct organic connection with the archicarp or ascogenous hyphae.

Early in the history of the archicarp there are developed also paraphysis-like structures, termed setae, which originate far below the hymenium from vegetative hyphae, traverse the hymenium, and protrude beyond it as thick-walled, dark-colored spines. These spines are non-septate tubes which discharge at their tips a brown, glutinous secretion over the surface of the hymenium.

The terminal branches of the ascogenous hyphae push up to the base of the paraphysis layer, and there undergo typical crozier formation. The terminal portions of the hyphae are of smaller diameter than the cells nearer the archicarp. The tip of each branch contains two nuclei, and in some cases these are cut off from the remainder of the thread by a septum. The nuclear membrane is sharply defined and the nucleolus stains deeply. The two nuclei are in some cases closely approximated or actually in contact, while in others they lie relatively remote from each other. The tip of each branch of the ascogenous hyphae forms a single definite hook (figs. 14–21). Although irregular hooks (figs. 17, 18) are not infrequent, complex systems of hooks such as those described by CLAUSSEN (**17**) in *Pyronema confluens*, by BROWN (**11, 12**) in *Leotia*, *Lachnea*, and *Geoglossum*, and by MCCUBBIN (**53**) in *Helvella elastica* have not been found.

The two nuclei in the tip of the hypha at the time of crozier formation probably undergo conjugate division in the usual manner. Four nuclei (figs. 19–21) thus result. These drift apart, the uppermost pair passing into the bend of the hook, which then undergoes renewed growth and develops a prominent "dome cell" (fig. 21). The other pair of nuclei come to lie in such a position that one occupies the recurved tip of the hypha and the other the main body of the thread. The two septa frequently figured in

other Ascomycetes are then laid down, and the dome cell thus cut off develops into the ascus.

Ascus

The young ascus increases rapidly in size, and pushes upward among the paraphyses. It assumes a definite cylindrical shape, and its two nuclei, now closely approximated at its center, soon fuse (fig. 23). Fusion nuclei containing two nucleoli are frequently found (figs. 22, 23). After fusion the nucleus increases in size as the ascus enlarges. The two nucleoli evidently fuse, the fusion nucleolus being larger and staining deeply.

The chromatic material undergoes certain changes which call for special comment. The extrusion of chromatic bodies from the nucleus during synapsis or at early stages in meiosis is described by DIGBY (**23**) in *Galtonia candicans*, and by CARRUTHERS (**14**) in *Helvella crispa*. They state that these bodies may arise either from the nucleolus or nuclear framework. In both cases they are impregnated with chromatin. They are ejected forcibly through the nuclear membrane, and on escaping become definitely pyriform by constriction. They are sometimes drawn out behind into a fine thread and by means of this remain attached to the nucleus for a considerable time. Figures of these bodies given by CARRUTHERS resemble very closely similar bodies present in *R. undulata*. A comparison of the figures presented in the two cases shows them to be strikingly similar. However, the writer is unprepared to state that in *R. undulata* they actually represent ejected chromatin. It is certain that bodies taking the stain in a similar manner may be found in the cytoplasm of the ascus remote from the nucleus (figs. 22, 24, 27).

The mature ascus of *R. undulata* contains 8 unicellular hyaline spores. No attempt has been made to study the method of cutting out of the spores, nor has any critical examination been given to the nuclear divisions in the ascus.

General considerations

It is not necessary to review here the history of the development of our knowledge of the sexuality of the Ascomycetes. This task has been thoroughly accomplished by other workers. The earlier

papers bearing upon the subject are excellently reviewed by HARPER (**40, 41**), LOTSY (**50**), OVERTON (**56**), and GUILLIERMOND (**37**); while more recent literature has been discussed by FRASER (**29**), RAMSBOTTOM (**58, 59**), DODGE (**25**), and ATKINSON (**1**). It will prove profitable, however, to call attention to the more important general problems which are encountered in the investigation of the sexual phenomena in this group, and to review briefly the results of certain researches which bear directly upon our own study of *Rhizina undulata*.

The great difference of opinion which exists in the interpretation of the nuclear phenomena in the ascogonium, ascogenous hyphae, and asci has resulted in general uncertainty as to the real essence of sexuality in the Ascomycetes. Certain investigators maintain that the fusion nucleus of the ascus is the product of two successive nuclear fusions, the first of these taking place usually in the archicarp and constituting the sexual fusion, while the second occurs in the young ascus and is regarded as vegetative. HARPER (**41**) explains the occurrence of this second fusion in the ascus as an attempt on the part of the fungus to maintain the nucleocytoplasmic relation or equilibrium in the cell, a large cell such as the ascus requiring a large nucleus (DANGEARD **19**, HARPER **38**, WINGE **67**). He states further that his researches indicate "that the fusion of the nuclei in the young ascus does not result in doubling the number of chromosomes as they appear in the succeeding divisions." Other investigators of this group, however, maintain that the fusion nucleus of the ascus is as the result of the two fusions necessarily tetraploid, and undergoes during the progress of the three divisions in the ascus a double reduction, the haploid number of univalent chromosomes being reached in each of the 8 resulting nuclei. FRASER (**28** *Humaria rutilans*) and others (FRASER and BROOKS **31** *Humaria granulata*, *Ascobolus furfuraceus*, *Lachnea stercorea*, FRASER and WELSFORD **32** *Otidea aurantia*, *Peziza vesiculosa*, and CARRUTHERS **14** *Helvella crispa*) state also that the third division in the ascus accomplishes the second reduction by a unique process termed brachymeiosis. In the later stages of this mitosis, according to their accounts, whole chromosomes are pulled toward the poles, the number in the telophase thus being reduced to one-half that in the prophase.

Many other investigators, however, maintain that the nuclear fusion in the ascus constitutes the only fusion in the life cycle, and state that the third division in the ascus is a typical vegetative mitosis. FAULL (**26** *Hydnobolites*, *Neotiella*) and CLAUSSEN (**17** *Pyronema confluens*) state that the same number of chromosomes is found in each of the three divisions in the ascus, and HARPER (**40** *Pyronema confluens*, **41** *Phyllactinia Corylea*), who describes a double fusion, also finds the chromosome number remaining constant.

Although many Ascomycetes have been examined in the endeavor to reach a satisfactory solution of the questions involved in this controversy, investigators are now as far as ever from agreement. The minute size of the sexual nuclei and the consequent difficulty encountered in demonstrating fusion renders misinterpretation easy. It is possible, as suggested by BROWN (**12**), that nuclear division in the ascogonium has been mistaken for fusion. Moreover, the presence of V-shaped chromosomes in the third division in the ascus in some species at least probably explains the differences in chromosome counts made by different investigators. It is possible also that coalescence of degenerating nuclei has been mistaken for a sexual fusion.

It will be admitted also that two lines of a priori argument have contributed to the general disagreement concerning the essential facts in the nuclear history of the Ascomycetes. One group of investigators maintains that two successive nuclear fusions in a single life cycle, resulting in the production of a fusion nucleus with the $4x$ chromosome number, followed by a double reduction embracing the remarkable process of brachymeiosis, constitute a phenomenon so unusual as to warrant skepticism and to demand absolute proof. Since no similar variation has been found in any other group of organisms they doubt its occurrence in the Ascomycetes.

The other school of workers lay great stress upon the presence of 8 spores in the ascus of so many Ascomycetes, and point out that even in asci containing fewer spores than 8 the production of 8 nuclei as the result of the triple division of the fusion nucleus has been described in practically every species investigated. This almost universal occurrence of the triple division in the ascus is ascribed

by them as due to the "quadrivalent character" of the chromosomes in the fusion nucleus, which renders 3 mitoses necessary for the return to the univalent condition. When fewer than 8 spores are formed, the supernumerary nuclei degenerate (HARPER **41** *Phyllactinia Corylea*) or two or more nuclei are incorporated in one spore (WOLF **68** *Podospora anserina*). When many-spored asci are formed, additional vegetative nuclear divisions take place following the triple division.

In *Eremascus fertilis* (STOPPEL **60,** GUILLIERMOND **36**) the triple division occurs, but, as ATKINSON (**1**) has pointed out, there is here certainly only a single fusion, the antheridium and ascogonium being uninucleate and the fertilized ascogonium functioning as the ascus after fusion has occurred. Also in *Dipodascus albidus* (JUEL **47**) and *Endomyces Magnusii* (GUILLIERMOND **36**) essentially the same process takes place; a single nuclear fusion precedes spore formation, and the fertilized ascogonium functions directly as the ascus. In *Endomyces Magnusii*, moreover, according to GUILLIERMOND, only two divisions occur in the ascus and 4 uninucleate spores are formed.

The triple division in the ascus resembles very closely the process in the Basidiomycetes by which the basidium in some species (FRIES **33** *Nidularia pisiformis*, LEVINE **49** *Boletus* spp., *Strobilomyces strobilaceus*) produces as the result of 3 successive nuclear divisions 8 nuclei, which appear in 4 binucleate spores. Since in these cases the 3 divisions follow one another rapidly and a rest period then ensues, the resemblance to the process in the Ascomycetes is marked. LEVINE describes the third division as taking place always in the spore, and states that in *Boletus albellus* a fourth division occurs, the resulting 4 spores being tetranucleate. FRIES states that in *Nidularia pisiformis* uninucleate spores are never found, and says that immediately upon the entrance of the nucleus completely into the spore a spindle is seen forming. He believes that the nucleus while migrating through the canal of the sterigma is already in the prophase of division. When it reaches the spore the equatorial plate is formed at once. MAIRE (**51**) in *Clavaria rugosa* and *Cantharellus cinereus* figures the third division as taking place in the basidium itself.

The questions involved in the study of the nuclear history of the Ascomycetes will never be satisfactorily answered by a priori argument. The careful examination of a large number of representatives of this group presenting peculiarly favorable material for investigation, and the comparison of the data obtained with those available for other groups will, however, go far toward explaining the discrepancies in conflicting accounts and toward answering vexing questions to the satisfaction of all students.

The greatest variation is evident in the morphology of the sexual apparatus in the Ascomycetes even in forms in which the gross structural characters of the ascocarp are very similar. The published evidence would seem to show, moreover, that a certain amount of variation in the unfolding of the sexual phenomena may be encountered in the investigation of even a single species.

In *Pyronema confluens* the sexual phenomena have been variously described. HARPER (**40**) gives in detail the passage of the male nuclei from the antheridium into the ascogonium, their fusion there in pairs with the female nuclei, the migration of the fusion nuclei into the ascogenous hyphae, and later a second fusion in the ascus. CLAUSSEN (**16, 17**) also describes the entrance of the antheridial nuclei into the ascogonium, but states that they merely pair there with the female nuclei without fusion. These pairs of nuclei then migrate into the ascogenous hyphae where they divide conjugately, two nuclei ultimately fusing in the ascus to give a fusion nucleus with the diploid number of chromosomes. This demonstration by CLAUSSEN of conjugate divisions in the ascogenous hyphae is especially noteworthy, since these divisions in the undifferentiated portions of the hyphae have not been demonstrated elsewhere in the Discomycetes. Since these nuclei divide conjugately, there is good reason to feel that they are linked together by a sexual attraction. FRASER (**30**), however, says that "the phenomenon of conjugate division is probably but a special example of the very general fact that nuclei present in the same cell usually divide simultaneously" (FROMME **34**, OLIVE **55**). WELSFORD (**66**) suggests that the paired condition of the nuclei may be merely the response to the physiological conditions usually found in rapidly developing hyphae. VAN TIEGHEM (**62**) grew under cultural con-

ditions a form which he stated to be *Pyronema confluens* and was able to develop normal or rudimentary antheridia or to suppress them entirely, while the ascogonia developed normally under all conditions. DANGEARD (**22**) found in what he regarded as the same species that even in cases in which the antheridium fuses with the trichogyne the male nuclei degenerate *in situ*, and fail to enter the ascogonium. BROWN (**10, 13**), working with a strain which he has named *Pyronema confluens* var. *inigneum*, found that the ascogonia and antheridia fail to fuse, and states that only one nuclear fusion, that in the ascus, occurs in the life cycle. He also examined the parent species, and states that in it he found migration of male nuclei into the ascogonium. *Pyronema confluens* var. *inigneum*, according to the account of BROWN, differs from the parent species physiologically also in that it grows freely upon an unsterilized substratum. The variation in the accounts of the different workers who have examined this species would seem to show that in this form the degeneration of the antheridium is now taking place. On account of the small size of the nuclei the demonstration of fusion in the ascogonium, however, is extremely difficult and it is possible that two investigators might reach a different conclusion from the examination of a single set of slides.

The writer feels that neither in *Pyronema confluens* nor in any other Ascomycete have two successive nuclear fusions in a single life cycle been conclusively demonstrated. It is evident that we cannot depend upon a critical examination of the nuclear divisions in the ascus to tell whether or not one or two fusions have occurred, since here also a fundamental difference in interpretation exists. Although FRASER and her co-workers figure and describe brachymeiosis in several species, HARPER and others find the chromosome number remaining constant throughout the three divisions in the ascus.

Summary

1. The sexual process has not heretofore been studied in any member of the Rhizinaceae. The examination of *Rhizina undulata* Fries is therefore of considerable interest.

2. Material for study was collected at Ithaca, New York, and a paper describing the origin of the apothecium in this species has already been published (**27**).

3. The vegetative mycelium is parasitic on the roots of trees, and develops profusely in the soil. On the surface of the ground or on parasitized roots minute primordia of fruit-bodies are developed. These are composed of undifferentiated hyphae which form at the periphery a somewhat indefinite palisade layer.

4. After the ascocarp primordium has attained a diameter of approximately 1 mm., certain hyphae near its center are transformed into archicarps. As many as 8 archicarps may be developed in a single ascocarp.

5. The individual archicarp develops by the rapid growth and transformation of an ordinary multicellular hypha. Its cells are multinucleate from the first. The nuclei increase greatly in number by repeated division and the archicarp soon takes on a dense opaque appearance.

6. An antheridium is absent.

7. The archicarp develops in some cases as a loose coil, and in others winds irregularly among the other hyphae, but tight coils have not been found. The number of cells in a single archicarp has been found to vary from 10 to 19 or more.

8. The terminal cell of the archicarp is small and attenuated, and at maturity shows disorganized protoplasmic contents. It has been here from analogy termed the trichogyne, but it certainly does not function.

9. As the archicarp approaches maturity a single, very prominent, deeply staining, hemispherical or convex pad appears on each side of the transverse septa. These pairs of deeply staining pads apparently represent a swelling of the wall due to gelatinization at that point. They later fuse and finally disappear, leaving a large pore in the septum.

10. Approximately one-half of the cells of the archicarp lying at the center of the coil now put out ascogenous hyphae. The remaining basal and apical cells fail to bud, and their nuclei and cytoplasm flow through the pores in the transverse septa into the ascogonial cells, and thence into the ascogenous hyphae.

11. With the outward flow of nuclei and cytoplasm into the ascogenous hyphae, the cytoplasm in the ascogonial cells of the archicarp becomes pronouncedly vacuolated. The nuclei are then seen to lie in pairs. In preceding stages the dense nature of the protoplasm and the crowding of the nuclei render the demonstration of a paired condition extremely difficult. Pairs of nuclei in the archicarp have been seen only in cells giving rise to ascogenous hyphae.

12. Careful search has failed to demonstrate stages of nuclear fusion in the ascogonial cells or in the ascogenous hyphae.

13. Paired nuclei are also present in the ascogenous hyphae. Neither conjugate nor simple divisions have been demonstrated.

14. Crozier formation takes place, but elaborate systems of hooks at the ends of the ascogenous hyphae have not been found. Nuclear fusion occurs in the young ascus.

DEPARTMENT OF PLANT PATHOLOGY
CORNELL UNIVERSITY

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EXPLANATION OF PLATES III AND IV

All the figures were drawn with the aid of an Abbé camera lucida, and various combinations of lenses were used. The drawings have been reduced two-sevenths in reproduction. Figs. 1–4 were built up from consecutive sections of a series, two sections each being used for figs. 1 and 2, and three sections each for figs. 3 and 4. This was necessitated by the fact that the archicarp rarely lies for any considerable portion of its length in the plane of one section.

Strictly speaking, however, these drawings are not composite, since the individual cells were outlined as they appear in a single section. In fig. 2 the terminal 6 cells were outlined from one section, and the basal 3 from the adjacent section. All of the central portion of the archicarp shown in fig. 3 was outlined from one section, although portions of these cells appear in the two adjacent sections. This explains the presence in the drawings of the deeply staining pads or open protoplasmic connections at certain septa and their absence at others where they lie outside the plane of the optical section. In those cases in which they are not shown, the examination of other optical sections usually shows either a pad or a pore, but in some cases they are obscured by the dense overlying protoplasm of one or the other of the adjacent cells. In fig. 4, due to the absence of winding in the archicarp, many of the open protoplasmic connections appear in one plane. In drawing the terminal cell of the archicarp shown in fig. 3 an exception has been made to the general method of treatment. This cell on account of its coiled nature cannot be shown satisfactorily in a single plane, but since it lies wholly in one section it has been possible to draw it in perspective. The nuclei shown in figs. 1–4 have not been outlined with the camera lucida, and the writer has attempted to show in the cells of these archicarps merely the relative number and size of the nuclei, not their exact position. The dense nature of the cytoplasm at these stages, the crowding of the nuclei, and the use of several optical sections in the preparation of the drawings renders a faithful portrayal of the nuclei impossible. The remainder of the drawings (figs. 5–27) have been made from a single optical section and the nuclei and other cell contents are accurately reproduced.

PLATE III

FIG. 1.—Terminal portion of young archicarp of *Rhizina undulata* Fries, ×500; note dense protoplasmic contents, numerous nuclei, and deeply staining convex pads on transverse septa of lower and more nearly mature cells; the fact that the terminal cells are long and slender and contain relatively few nuclei indicates the origin of the archicarp from a vegetative hypha.

FIG. 2.—Terminal portion of a somewhat older archicarp, ×500; note attenuated terminal cell, trichogyne; deeply staining pads and open protoplasmic connections cannot be seen on all septa since they lie outside plane of section.

FIG. 3.—An entire archicarp nearing maturity, ×500; 2 ascogonial cells have already begun to put out ascogenous hyphae; deeply staining pads are prominent on several septa; open protoplasmic connections have resulted from their disappearance on others.

FIG. 4.—An entire archicarp contrasted in size with ordinary hyphae of ascocarp, ×500; here open protoplasmic connections are visible at practically every septum.

FIG. 5.—Cells in basal region of archicarp at time of general flow of nuclei and cytoplasm into ascogonial cells, ×500.

FIG. 6.—Cells in apical region of another archicarp when this phenomenon is taking place, ×500.

FIG. 7.—Ascogonial cells of archicarp putting out ascogenous hyphae, ×500; note paired nuclei, and persistence of a single pair of deeply staining pads.

PLATE IV

FIGS. 8, 9.—Transverse sections through budding ascogonial cells at points between places where ascogenous hyphae arise, ×1315; note vacuolated cytoplasm and paired nuclei; no fusion stages have been observed; in those cases in which a solitary nucleus appears, its companion lies either above or below.

FIGS. 10, 11.—Transverse sections through budding ascogonial cells, ×1315; in these cases ascogenous hyphae at their point of origin lie in plane of section; note paired condition of nuclei in ascogenous hyphae.

FIG. 12.—Ascogenous hyphae midway between ascogonial cells and developing hymenium, ×1315.

FIG. 13.—Terminal branches of ascogneous hypha just preceding crozier formation, ×1315.

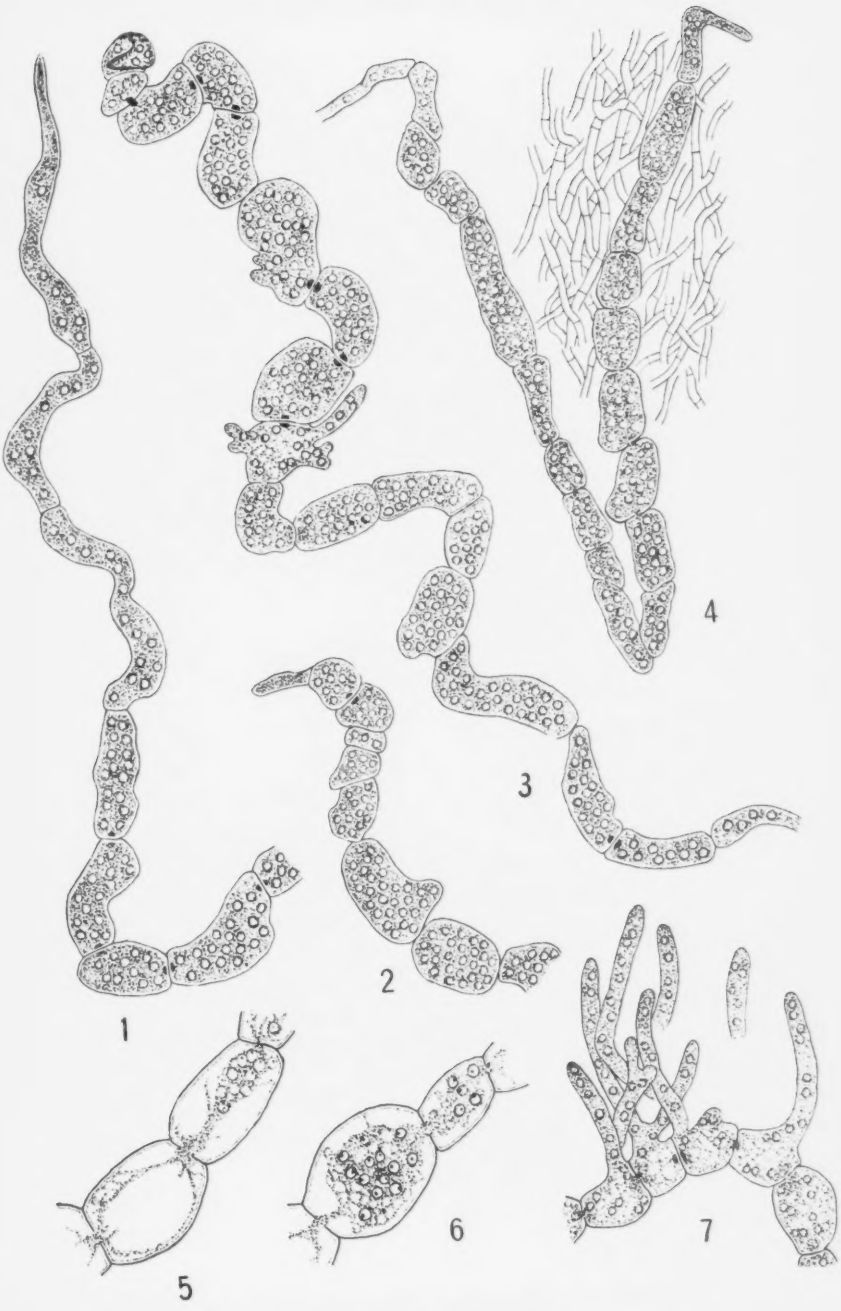
FIGS. 14–18.—Ascus hooks containing single pair of nuclei preceding conjugate division, ×1315.

FIGS. 19–21.—Ascus hooks containing 4 nuclei after conjugate division has taken place, ×1315.

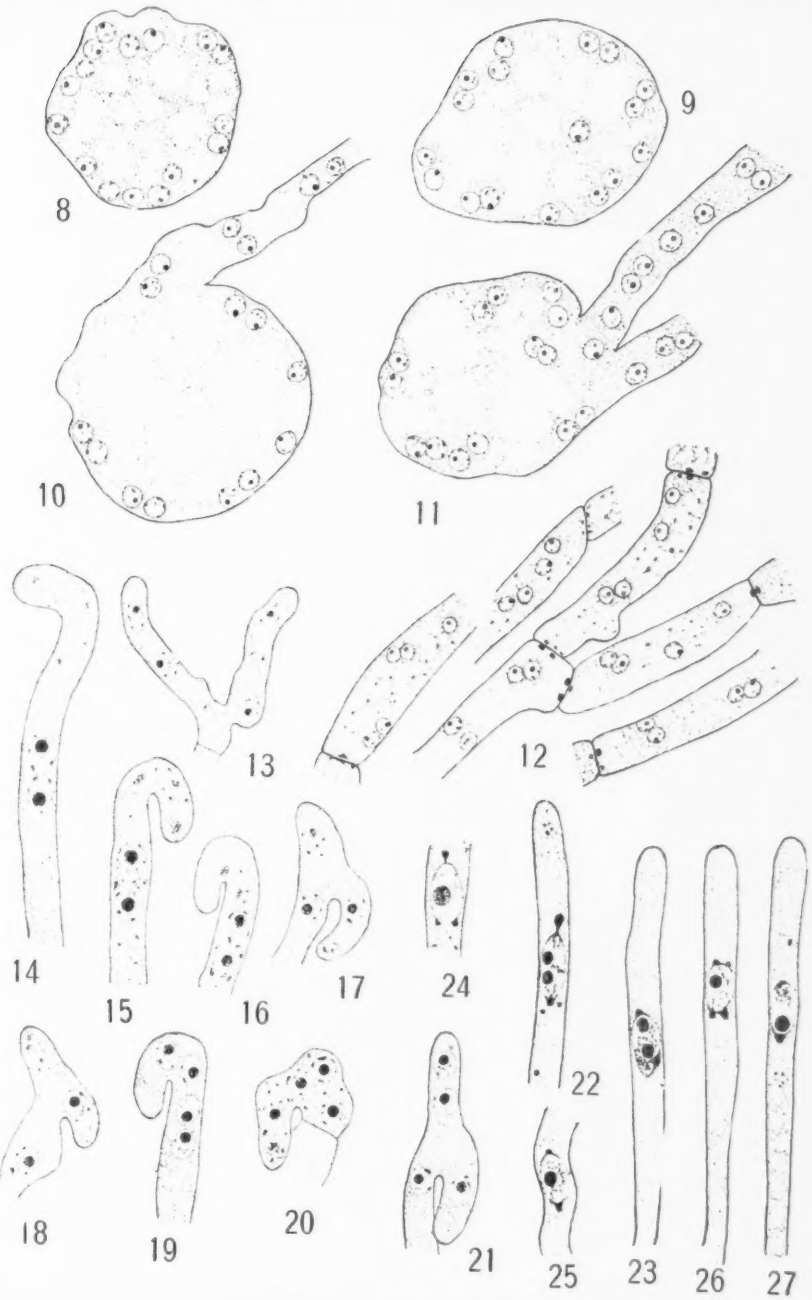
FIGS. 22, 23.—Young asci, fusion nucleus in each still showing two nucleoli, ×830.

FIG. 24.—Fusion nucleus containing single fusion nucleolus, ×1315.

FIGS. 25–27.—Young asci showing fusion nucleus with single nucleolus, ×830.



FITZPATRICK on RHIZINA



FITZPATRICK on RHIZINA

SOME MELIOLICOLOUS PARASITES AND COMMENSALS FROM PORTO RICO

F. L. Stevens

(WITH PLATES V AND VI AND FIVE FIGURES)

The genus *Meliola* is distinctly tropical and within the tropics is most abundant in humid locations, although there are many species found in arid regions. It is chiefly in the warm humid locations that the species are accompanied and overgrown by other fungi; frequently so heavily overgrown as to entirely obscure the *Meliola* itself, stop spore production, and even the presence of the *Meliola* may be proved only by very careful search. The exact relation which these fungi bear to the *Meliola* is not known. True parasitism, owing to the dark color of the mycelium, is much more difficult to demonstrate than in the case of *Cicinnobolus* on the Erysiphaceae, so familiar in temperate climates. It is extremely probable that all of the forms except the last considered are parasitic. This last is probably merely an accidental associate. Some of the pycnidial forms were formerly regarded as belonging to the *Meliola* cycle, but more recent studies do not support this view. Two of the hyphomycete genera have been regarded by some students of *Meliola* as the conidia of *Meliola*, while others treat them as independent fungi, and still others evade the question.

It is not possible to regard the ascigerous forms of *Microthyrium*, *Dimerium*, *Podosporium*, *Calonectria*, etc., as genetically connected with the *Meliola*, nor is there any more reason for assuming genetic connection in the case of any of the forms mentioned later. They may be merely commensals favored by the environment, but there is very strong circumstantial evidence that they are parasitic, and there is no sufficient reason to regard any of them as belonging to *Meliola*. The special statement in this connection relating to *Arthrobotryum* and *Helminthosporium* is given later. The specimens upon which this article is based are filed under the *Meliola* host, and are deposited as indicated in an article by Miss Young.[1]

[1] Young, E., Mycologia 7:143. 1915.

PEZIZACEAE

BELONIDIUM LEUCORRHODINUM (Mont.) Sacc. on *Meliola chiococcae* Stev. on *Chiococca alba*, 7325, Hormigueros; on *Meliola tortuosa* Wint. on *Piper umbellatum*, 5656, Jajome Alto; on *Meliola rudolphiae* Stev. on *Rudolphia volubilis*, 4835, Maricao, 5439, Luquillo Forest.

This fungus is very inconspicuous and would escape observation except under a good lens. It then appears as numerous small pale disks upon the *Meliola* mycelium. Although the present specimens agree well with the description given in the *Sylloge Fungorum*, there is still some doubt as to its generic position; indeed, the limits of the genera *Calloria* and *Belonidium* are of such nature that this fungus might well be placed in either of them. Although septation of the spores was not definitely proved, there is a segmentation of the protoplasm in the spores which seems to indicate beginning of septation.

PERISPORIACEAE

Perisporium paulliniae, sp. nov. (text fig. 1).—Mycelium inconspicuous. Perithecia few in centers of old *Meliola* colonies. Asci fasciculate from base of perithecium, 100×25 μ, clavate, 8-spored; spores inordinate, clavate to somewhat irregular-cylindrical, 5-septate, 44×10 μ, usually with two cells decidedly thicker than the others; these thickened cells the second and third from one end. Ends obtuse, constriction medium, color dark smoky.

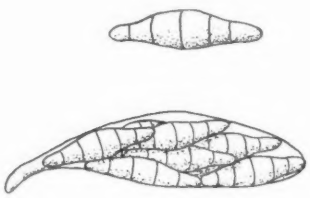


FIG. 1.—*Perisporium paulliniae* on *Meliola hessii*, no. 1207 (type).

On *Meliola hessii* Stev. on *Paullinia pinnata*, 1207 (type), Mayagues.

Perisporium meliolae, sp. nov. (text fig. 2).—Mycelium scant, inconspicuous, growing upon *Meliola* mycelium. Perithecia clustered in the central regions of old *Meliola* colonies, lenticular, slightly taller than broad, 230–280 μ thick, 312 μ high, surface closely covered with short tubercles. Asci numerous, fascicled, 8-spored, cylindrical. Paraphyses absent. Spores 7–14×31–44 μ,

brown, usually 3-septate (sometimes less), often tapering toward one end, that is, ends not equally thick. Ends obtuse, median constriction greater than the others, wall thick, 2–3 μ, surrounded by a distinct, thin, gelatinous coat.

On *Meliola compositarum* var. *portoricensis* Stev.; on *Eupatorium portoricense*, 6032 (type), 6557, 6056, 6003, 6861, 6031, 6866, Dos Bocas near Utuado, 5192, San Sebastian.

The presence of the 8-spored, fascicled, long, narrow asci and the absence of the typical *Meliola* mycelium distinguish this *Perisporium* from *Meliola*. The peculiar lenticular perithecia, which stand on edge, are also characteristic. Associated with this species are conidiophores and conidia, and it is entirely probable that it may be the ascigerous stage of one of the Meliolicolous species of *Helminthosporium*.

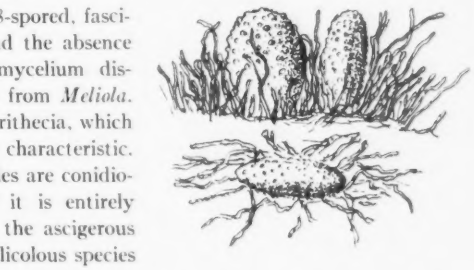


FIG. 2.—*Perisporium meliolae* on *Meliola compositarum* var. *portoricensis*, no. 6032 (type); flattened perithecium; views from side, edge, and from above; an ascus and single spore.

These two species of *Perisporium* are especially interesting, since, growing on *Meliola*, their perithecia are likely to be taken for the *Meliola* perithecia, which they closely resemble in character of spores. They are readily separable, however, from *Meliola* by the absence of the characteristic *Meliola* hyphopodia and by the presence of the fascicled, 8-spored asci which perhaps do not really occur in true *Meliola*.

DIMERIUM PICEUM (B. and C.) Thiessen Bot. Centralbl. Beih. **29**:66. 1912.—*Asterina picea* B. and C.; *Dimerium microsporium* Speg.; *D. meliolicolum* Speg.; *D. guineri* R. Marie; *Dimerosporium tropicale* Speg.; *D. clidemniae* P. Henn.; *D. hyptidicola* P. Henn.; *D. dendriticum* A. and S.

On *Meliola glabra* var. *psychotriae* Stev. on *Psychotria* sp., 5032, Quebradillas; on *Palicourea* (?) 1070, Mayaguez. On *Meliola bicornis* Wint. on *Micbomia supina*, 4532, Cataño. On *Meliola glabroides* Stev. on *Piper aduncum*, 4802, Maricao. On *Meliola tortuosa* Wint. on *Piper umbellatum*, 3379, Maricao. On *Meliola ipomoeae* E. Heller's coll. no. 6285 appears to be the same, but the available material is scarce. On *Meliola compositarum* E. var.

portoricensis Stev. on *Eupatorium portoricense*, 6031, Utuado. On *Meliola pteridicola* Stev. on *Anemia adiantifolia*, 7269, Quebradillas, 8015, Utuado, 7814, Rio Tanamá. On *Meliola panici* E. on *Panicum glutinosum*, 4801, Maricao; on Gramineae indet., 6796, Arecibo; on *Lasiacis divaricata*, 4298, Manati. On *Meliola paulliniae* Stev. on *Casearia ramiflora*, 6683, St. Ana, 5844, San German.

While slight variations occur, it seems best to do as THIESSEN has done and regard the variants as of one species, and to unite the several species which were originally described as distinct.

MICROTHYRIACEAE

Members of this family abound on *Meliola*. The manner in which the mycelium of the parasite clothes the mycelium of the *Meliola* in a sheath is particularly striking. In some instances only single *Meliola* branches, portions of a colony, are so coated; in other cases the whole *Meliola* colony is covered. Sometimes the sheathing is limited to the host mycelium, but in older specimens the sheath expands into a continuous sheet or crust. The perithecia are very numerous, on young colonies as very small developing structures, on old ones as dense clusters of mature perithecia. Several species of *Meliola* have been described as having this crustose structure, and it is very probable that all such cases represent merely parasitized colonies. Generic and specific determination of the specimens is deferred for consideration in a separate paper dealing with the family.

HYPOCHREALES

Pseudonectria pipericola, sp. nov.—Mycelium closely appressed on the *Meliola* mycelium. Perithecia numerous, minute, 100–125 μ in diameter, pink, with a few setae around the ostiole. Setae short, 20–30 μ, obtuse, continuous; asci cylindrical, 50×5–7 μ, 8-spored, 1-seriate, sometimes oblique; paraphyses none; spores elliptical or oblong, obtuse, continuous, hyaline, 9–10×3–4 μ.

On *Meliola tortuosa* Wint. on *Piper umbellatum*, 5656 (type), Jajome Alto, 3578, 3508, 3507, Añasco, 7916, 7848, Rio Tanamá; on *Piper marginatum*, 7777, 7842, Rio Tanamá.

This is closely related to *Nectria mycelophila* Pk. described on decaying fungi, but differs in having smaller spores, different shape of asci, and in the presence of setae around the ostiole.

Nectria meliolicola, sp. nov.—Amphigenous, spot none, mycelium white, closely appressed to the *Meliola* mycelium and to the leaf, usually coextensive with the *Meliola* or slightly exceeding it. Perithecia very minute, 50–60 μ at center or near edge of colony, hyaline, hairy at apex, hairs 15 μ long. Asci ovate to elliptical, obtuse, stipitate, 40–45×11–14 μ; spores 1-seriate, oblique, 1-septate, hyaline, linear, 24–28×3–4 μ, acute.

Associated with an undetermined *Fusarium* on *Meliola paulliniae* Stev. on *Casearia sylvestris*, 1051, Mayaguez (type).

It is impossible to distinguish the mycelium of this fungus from that of the *Fusarium*, and it is probable that the two are one. The spot caused on the leaf is not due to these fungi but to the *Meliola*.

Nectria portoricensis, sp. nov.—Colonies approximately circular on *Meliola*, 3–7 mm. in diameter, white, central portion bearing perithecia, outer part sterile. White mycelium covering each *Meliola* strand with a shaggy coat. Perithecia red, small, 160 μ, smooth; asci 25–36×8 μ, obovate, obtuse; spores 1-seriate, oblique, oblong, hyaline, pale to green, 1-septate, 12×3 μ, obtuse.

Distinguished from *N. pipericola* P. Henn. by absence of perithecial setae, shape and size of spores, and by habit of the sterile mycelium; from *N. bakeri* Rehm. by spore characters. On *Meliola rectangularis* Stev. on *Banisteria laurifolia*, 1001, Jayuya (type).

This fungus differs strikingly from all other Porto Rican Nectriaceous fungi in the beautifully arranged, dense, shaggy, white mycelial coating which drapes with geometrical accuracy every affected strand of the *Meliola* mycelium. A white mycelium of appearance similar to this was abundant, overgrowing colonies of *Meliola melastromacearum* Speg. no. 7037, but no perithecia were seen.

CALONECTRIA MELIOLOIDES Speg.

On *Meliola compositarum* var. *portoricensis* Stev. on *Eupatorium portoricense*, 6003, 6032, 6557, 6830, 6031, 6861, 6866, 7053, 8102, Dos Bocas below Utuado, 5102, San Sebastian; on *Eupatorium odoratum*, 6001, 6056, 6574, Utuado. On *Meliola paulliniae* Stev. on *Casearia sylvestris*, 3020, 1200, Mayaguez. On *Meliola hessii* Stev. on *Paullinia pinnata*, 1207, Mayaguez.

Spores on this host showed a pale olivaceous tint. The form on *Eupatorium portoricense* usually forms a mat of densely felted mycelium and may be a distinct species. On *Meliola monensis* Stev. on *Amyris elemifera*, 6158, Mona Island.

CALONECTRIA ERUBESCENS (Rob.) Sacc.

On *Meliola bicornis* Wint. on *Meibomia supina*, 5820, Adjuntas. On *Meliola tortuosa* Wint. on *Piper umbellatum*, 5692, Jajome Alto. On *Meliola cupaniae* Stev. on *Cupania americana*, 9318, Mayaguez.

Calonectria graminicola, sp. nov.—Mycelium growing over the *Meliola* and covering it with a white coat, usually coextensive with the *Meliola*. Perithecia few to numerous, reddish, pale when dry, globose, 200–225 μ, cells irregular, 10–18 μ in diameter. Perithecial setae rather numerous, tapering regularly to an obtuse apex, not septate, base not bulbous although swollen slightly just above attachment, 75 μ long, 15 μ wide at base. Asci numerous, 8-spored, 75×7–8 μ, cylindrical; paraphyses threadlike, abundant. Spores 3-septate when mature, hyaline to pale straw colored, straight, curved or sigmoid, acute at each end, 30–36×5 μ.

On *Meliola panici* Earle on *Lasiacis compacta*, 4663 (type), Utuado; on *Lasiasis divaricata*, 4298, Manati, 6796, Arecibo. On *Meliola andirae* E. on *Andira jamaicensis*, 5269, Manati.

This fungus resembles *C. melioloides* Speg., but may readily be distinguished by its non-septate setae and the shape of the spores.

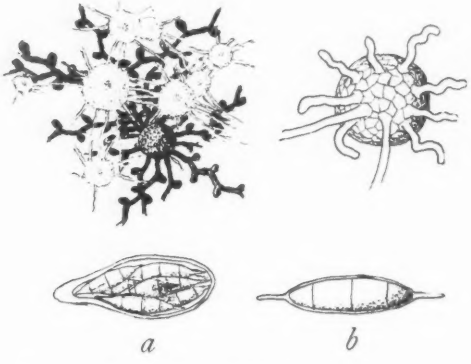


FIG. 3.—*Paranectria meliolicola*, sp. nov.: *a*, ascus, *b*, single spore.

One of the Hypocreales, probably a *Calonectria* but immature and therefore not determinable, was profuse on *Meliola toruloidea* Stev. on *Cassia quinquadrangulata*, 8394, Jajome Alto.

Paranectria meliolicola, sp. nov. (text fig. 3).—Mycelium hyaline, of threads 5 μ thick, which closely surrounded the *Meliola* mycelium. Perithecia produced in abundance, 75–120 μ in diameter, red to pale, with few setae, 15–30–50 μ long. Asci clavate to ovate, obtuse, 8-spored,

thin-walled, 45–55×25–40 μ. Spores hyaline, oblong to oblong-elliptical or with one side nearly straight and the other arched; ends obtuse, a rigid, obtuse, straight, sometimes slightly curved awn at each end. Spores 3-septate, 2 outermost septa arched strongly outward, spore body 7–10×22–30 μ; awn 2×8 μ.

On *Meliola tortuosa* Wint. on *Piper umbellatum*, 3634, Maricao (type). On *Meliola glabroides* Stev. on *Piper aduncum*, 4930, Lares.

This interesting genus differs from *Calonectria* only in the possession of appendaged spores. There are less than 10 species, none of which agrees at all closely with ours. *P. albo-lanata* Speg. described on bamboo does agree closely in spore character but not otherwise. The fungus without the use of a lens is barely visible.

Paranectria miconiae, sp. nov. (text fig. 4).—Perithecia globular, gray to white, 100–150 μ in diameter, with a whorl of basal hairs which are non-septate, thick-walled, obtuse; in length equal to

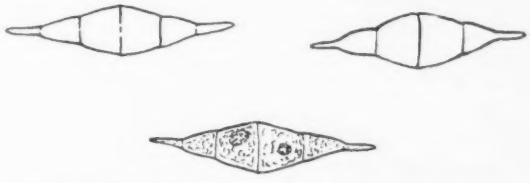


FIG. 4.—*Paranectria miconiae*, sp. nov.: *a*, habit sketch showing *Paranectria* overgrowing *Meliola*; *b*, perithecium seen from below, showing basal hairs; *c*, spores on microthyriaceous fungus on *Miconia*; no. 6705.

half the diameter of the perithecium. Asci numerous, clavate to ovate, obtuse, thin-walled, 60×12–15 μ. Spores fusiform, strongly thickened in middle and tapering equally to each end. Almost long diamond-shaped in outline, with a straight, cylindrical awn at each end, 32×7–8 μ including awns, 3-septate. Spores in mass, or in ascus, slightly greenish. Paraphyses threadlike, short.

On *Miconia* on Microthyriaceous fungus, 6705, Yabucoa (type).

SPHAEROPSIDALES

Naemosphaera hyptidicola, sp. nov.—Pycnidia spherical, about 60 μ in diameter, black, mycelium inconspicuous. Rostrum long, often 500 μ, 17 μ thick, dark, tip pale, composed of parallel hyphae. Spores straw colored, oblong, obtuse, 5–6×2.5–3 μ.

On *Meliola hyptidicola* Stev. on *Hyptis*, 5760, Monte de Oro (type).

This does not agree with any pycnidial forms given by GAILLARD as occurring on *Meliola;* 3 only of his are yellow spored, namely, those on *M. ganglifera*, *M. cladotricha*, and *M. furcata*. The first two have large spores, and the length of neck of the pycnidium on my species does not agree at all with any of the three. *N. hyptidicola* is also distinct from the rather closely allied genus *Cicinobella* recorded as parasitic on *Parodiella*.

Coniothyrium glabroides, sp. nov.—Pycnidia small, 50–90 μ, brown, ostiole distinct, no beak; mycelium inconspicuous; spores brown, 4–5×3.5 μ, obtuse, oblong.

On *Meliola glabroides* Stev. on *Piper aduncum*, 4802 (type). On *Meliola tortuosa* Wint. on *Piper umbellatum*, 3379, Maricao; also on no. 6258 of the Heller collection and on *Meliola compositarum* E. and no. 6185 of the Heller collection. On *Meliola guareicola* Stev. on *Guarea trichilioides*, 8166, Las Marias. On *Meliola arecibensis* Stev. on *Acalypha bisetosa*, 6547, near Utuado. On *Meliola compositarum* var. *portoricensis* Stev., 6032, on *Eupatorium portoricense*.

This fungus bears resemblance to *Cicinobella*, but the ostiole does not protrude. The spores too are different in size from the only species of that genus described. Specimens on *Meliola panici* E. on *Lasiacis divaricata*, no. 4298, Manati, agree closely with the preceding except that the spores are hyaline. I take them to be immature and place the specimens under this name. The same is true of specimen 7269, Quebradillas, on *Meliola pteridicola* Stev. on *Aneimia adiantifolia*.

In the closely allied genus *Chaetophoma* the following species have been described on *Meliola* and related genera.

C. foeda Sacc. on *Capnodium*, *C. penzigi* Sacc. on *M. penzigi*, *C. citri* Sacc. on *M. citri*, *C.*(?) *ampullula* Speg. on *M. dubia*, *C.*(?) *asterinum* Speg. on *Asterina* sp., *C. perpusilla* Speg. on *Asterina pseudopelliculosa*, *C. meliolicola* Speg. on *Dimerosporium*.

GAILLARD mentions pycnidial fungi on the following species of *Meliola: M. ganglifera*, *M. cladotricha*, *M. penicilliformis*, *M. ambigua*, *M. desmodii*, *M. furcata*, *M. dichotoma*.

MONILIALES

Acremonium meliola, sp. nov.—Mycelium copious, white to salmon colored, forming cottony blotches on leaves where it overgrows *Meliola*, fine, 3 μ, septate, hyaline. Conidiophores smiliar to the mycelium, erect or ascending, often simple or with dichoto-

mous or verticillate branching. Conidia terminal and solitary or more rarely in clusters, pear-shaped, rounded or obtuse at base, acute at apex, 15–20×5–7 μ. Spores, mycelium, and conidiophores encrusted with minute granules.

On *Meliola paullinae* Stev. on *Paullinia pinnata*, 376, Vega Baja.

This is clearly differentiated from the other species by the shape of the spores.

Arthrobotryum Ces.

The forms here under discussion are characterized by fuscous to dark mycelium, conidiophores, and spores; conidiophores long, straight, and fascicled in typical coremia. The coremia are in the main straight and rigid, the component fibers running approximately parallel and are firmly agglutinated. They are not sporiferous upon the lower parts, but possess a well marked, long, nonsporing stipe. The extreme distal parts of the coremia are usually swollen to more or less cylindrical or conical heads, although in some species the head is but poorly developed. The spores are elliptical or falcate, 2 or 3-septate, fuscous. Such structure clearly places these forms in the Stilbaceae-Phaeostilbeae-Phragmosporae. They are usually regarded as belonging to the genus *Podosporium*, and 3 species growing on *Meliola* have been described: *P. penicillium* Speg. (Fung. Arg. Pug. IV. n. 117), *P. penicillioides* Karsten and Roum. (Rev. Myc. **12**:77. 1890), *P. densum* Pat. (Jour. de Botanique **11**:373. 1897). Examinations of original figures of the type species of this genus (*P. rigidum* Schw. Syn. Amer. Bor. n. 2608, Trans. Am. Phil. Soc. n.s. 4) and of a specimen of ELLIS (N.A.F. no. 416), which agrees with description and type figure fully, shows the *Podosporium* coremium to be pleurogenous and without heads, and therefore to be clearly distinct generically from the forms under discussion.

Comparison with figures of the type species of *Arthrobotryum* Ces., *A. stilboideum* (Engler and Prantl, Die Nat. Pflanzenfam. **1**: pt. 1, *fig. 257D*), and with figures of later species placed in this genus (Jour. Linn. Soc. **35**:13. *pl. 1. figs. 13–15*. 1901) show complete generic agreement.

While these structures have been regarded by some as independent species of fungi growing as parasites upon *Meliola*, GAILLARD

and others who have followed him regarded them as belonging to *Meliola* and constituting one of its conidial forms. The question is very complex and difficult and reminds one of the old lichen arguments.

The undisputed facts are as follows: *Meliola* possesses a relatively coarse mycelium characterized by capitate and mucronate hyphopodia. This mycelium bears perithecia, sometimes setae. Occasional species sometimes have this coarse mycelium densely entwined with a very fine mycelium entirely without hyphopodia, more pale in color, and different in every way from the first. This fine mycelium gives rise to conidiophores, simple or coremioid. To all appearances two distinct fungi are present, as was assumed by the earlier authors. The ascospores on germination nearly always immediately give rise to the typical coarse mycelium. The conidia always give rise to the fine mycelium. GAILLARD (Le Genre *Meliola*, 1892, *pl. 3. fig. 2*), however, figures, and I have several times seen, ascospores which have germinated by a somewhat finer mycelium than usual, one devoid, so far as observed, of hyphopodia. He reasons from this that the two types of mycelium are from the same parentage, the ascospore, and that therefore the conidia belong to *Meliola*. This variation from the normal mode of germination is really all the evidence that he had for this conclusion.

I believe that this evidence fails completely for two reasons. First, the fine mycelium which GAILLARD figures originating from the ascospores and which I have studied closely is not at all like the conidiiferous mycelium; it is distinctly coarser, darker (facts which come out clearly in GAILLARD's own pictures; compare his *pl. 3, figs. 3a* and *2a* with *pl. 4, figs. 3* and *1d*), and moreover there is no evidence whatever that it does produce conidia. I regard it merely as a weak *Meliola* mycelium. Second, I find this abnormal, unusual type of germination on species of *Meliola* which show no conidia; notably on *M. andirae* (cotype slide) and *M. rudolphiae* (specimen no. 8698). These facts, together with a study of more than 700 collections, and extensive field and laboratory observations of *Meliola* embracing many of these conidial stages, convince me that the fine and the coarse mycelia are from distinct and independent fungi; that the conidia do not belong to *Meliola* but to a

fungus parasitic upon it; and, as just stated, that the stilboid conidial forms belong to the genus *Arthrobotryum*. That this conclusion has also been reached by SYDOW[2] is indicated by his description of *A. caudatum* on *Meliola* in 1909. The type specimen of *A. caudatum*, loaned to me by SYDOW, clearly is cogeneric with the various forms on *Meliola* which have heretofore been called *Podosporium*. I present the following synopsis of the Porto Rican forms of this genus:

KEY TO PORTO RICAN SPECIES OF *Arthrobotryum*

Coremia incasing the *Meliola* setae ..... *A. dieffenbachiae*
Coremia not incasing the *Meliola* setae
  Vegetative mycelium closely sheathing the *Meliola* mycelium ..... *A. glabroides*
  Vegetative mycelium not closely sheathing the *Meliola* mycelium
    Conidia long, elliptical, with no distinct beak cell ..... *A. penicillium*
    Conidia with distinct beak cell, basal cell, and two central cells
      A. caudatum

Arthrobotryum dieffenbachiae, sp. nov. (fig. 4).—Mycelium inconspicuous, scant, fine, pale, tufted around the bases of the coremia. Coremia often growing incasing the setae of the host, yellow, stalks 17–31 μ thick; total length 470–630 μ; apical portion either broadened into a fan-shaped brush or very narrow with lateral conidia; sporiferous part about 150 μ long. Conidia 3-septate, pale straw colored, pointed at each end, apical cell longer than basal cell, 35–38×3–4 μ.

On *Meliola dieffenbachiae* Stev. on *Dieffenbachia sequina*, no. 8077 (type), Dos Bocas below Utuado.

This species is the only one recorded which utilizes the setae of its host as supports for the coremia. The young coremia are somewhat transparent, and in them the supporting setae with their characteristically branched apices may be seen incased.

Arthrobotryum glabroides, sp. nov. (figs. 1–3).—Mycelium forming a loose network on the leaf surface but a close sheath over the *Meliola* mycelium, so dense as to partially obscure the hyphopodia, very fine, about 1 to 1.5 μ. Coremia straight, rigid, black, stalk about 24 μ thick, head 85 μ wide and 85 μ long, top-shaped. Total length of coremia 550 μ. Conidia narrowly elliptical, acute

[2] SYDOW in DE WIDEMAN'S, EMILE DE, Fl. Bas et Moy., Congo pl. III, fasc. 1, 1909.

at each end, dark brown when mature, 17–21×3.5 μ, typically 3-septate with the two terminal cells much smaller than the other cells.

On *Meliola glabroides* Stev. on *Nectandra patens*, no. 7595 (type), Mayaguez, 8867, Maricao.

This species is quite distinct from all others seen in the characteristic manner of sheathing its host, also in the shape of the conidia.

Arthrobotryum penicillium (Speg.), comb. nov.—*Podosporium penicillium* Speg. Fung. Puigg., n. 471.

On *Meliola panici* E. on *Panicum glutinosum*, 5672, 5746, 5560, Monte de Oro, 4375, Ponce, 5947, El Gigante, 4801, 8934, Maricao, 4368, El Alto de la Bandera, 4389, Utuado; on *Lasiacis divaricata*, 4298, Manati, 6810, Arecibo; on *Ichnanthus pallens*, 7441, Mayaguez, 5755, Monte de Oro; on Gramineae indet., 6796 Arecibo.

This form was originally described by SPEGAZZINI as the conidial stage of *Meliola penicillata*, and was later regarded by GAILLARD as the conidial stage of *M. calva*.

ARTHROBOTRYUM CAUDATUM Syd. (figs. 5–7).—A portion of the type specimen was sent to me by SYDOW, and its agreement with the specimens mentioned below is obvious.

On *Meliola pteridicola* Stev. on *Ancimia adiantifolia*, 8015, near Utuado. On *Meliola paulliniae* Stev. on *Casearia ramiflora*, 512, 7745, Vega Baja, 6306, Barcelonata. On *Meliola didymopanicis* P. Henn. on *Dendropanax laurifolium*, 8265, El Alto de la Bandera. On *Meliola glabra* B. and C. var. *psychotriae* Stev. on *Palicourea*, 6650, near Utuado, 468, Vega Baja; on *Psychotria pubescens*, 8032, near Utuado, 7741, 7732, Vega Baja; on *Psychotria bertiana*, 8646, 8566, 8528, El Gigante, 8278, 8673, El Alto de la Bandera; on *Palicourea*, 1070b, 316, Mayaguez; on *Psychotria* sp., 5032, Vega Baja, 5044.

What appears to be the same fungus was described as the conidial stage of *M. penicilliformis* by GAILLARD (Le Genre *Meliola*, 57, 1892). The species of *Meliola* itself being largely determined by its "conidial stage," its validity may well be doubted.

The specimens following seem to agree with the preceding in all respects except that the coremia are usually pale at tip, apparently soft, with the base tan or darker, the head merely a somewhat thickened apical region and the conidia very pale. It seems that the fungus on *Palicourea* shows transition forms which connect the two types.

On *Meliola hyptidicola* Stev. on *Hyptis lantanifolia*, 8130, Las Marias; on *Hyptis* sp., 5760, Monte de Oro. On *Meliola longipoda* Gaill. on *Anona montana*, 7561, Mayaguez. On *Meliola glabroides* Stev. on *Piper aduncum*,

9334, Martin Peña. On *Meliola ambigua* Pat. and Gaill. on *Lantana*, 6870, near Utuado.

The species on *M. glabroides* shows some variation in that the coremia usually taper gradually from the base to tip and are mounted upon a small tuft of radiating, fine, mycelial threads.

What appears to be the same species, although sterile, is on *Meliola psychotriae* E. on *Gonzalugunia spicata*, 9134, Miradero, 7592, Mayaguez, and on *Meliola melastomacearum* Speg. on *Miconia leavigata*, 8085, near Utuado, and on *Miconia racemosa*, 7636, 7414, Mayaguez. On *Meliola bicornis* Wint. on *Meibomia supina*, 8075, 8793, Maricao.

In addition to these the genus *Arthrobotryum*, under the name of *Podosporium*, has been noted as *P. densum* on *Meliola* sp. indet., as *P. penicillioides* on *Meliola tonkinensis;* while upon the following species of *Meliola* it has been described as a conidial stage: *M. echinata*, *M. insignis*, *M. glabra*, *M. quercina*.

Helminthosporium Link

Closely allied to *Arthrobotryum* is the genus *Helminthosporium*, which indeed, so far as it is parasitic upon *Meliola*, may be regarded as a simple form of *Arthrobotryum;* that is, in *Arthrobotryum* the conidiophores are fascicled in coremia, while in *Helminthosporium* the conidiophores are not so fascicled. In spore forms, in mycelial characters, and in all respects except the fasciculation of the conidiophores, the two genera as they occur on *Meliola* are identical. They bear the same relation to each other as do the form genera *Coremium* and *Penicillium*, a relation which emphasizes strongly the artificiality of a taxonomic system which separates widely forms which are in reality very closely related. The assumed genetic connection of *Helminthosporium* with *Meliola* has been sufficiently discussed under *Arthrobotryum*. The facts stated in that connection may be considered as applying equally to the forms now under discussion.

The Meliolicolous species of *Helminthosporium* are typical representatives of the genus. The mycelium is very fine, sometimes scant and diffuse, more often dense and matted. The conidiophores are commonly solitary, usually although not always much darker than the mycelium, and always considerably thicker than the mycelium. Their origin from the mycelium is well shown in

pl. 7, fig. 1 of GAILLARD'S *Le Genre Meliola*. They are in a few forms somewhat tufted, and what are apparently transition forms to *Arthrobotryum* occur. The conidia are in most species truncate at one end, beaked at the other. The beaked end is apical and the truncated end is basal, although the reverse condition might be assumed were the spores not studied *in situ* (see fig. 10); in the 3-septate forms the terminal cells are usually more pale than the central cells. The following key will serve to separate the Porto Rican species:

Conidia often more than 3-septate
  Conidiophores not very toruloid at tip ..... *H. glabroides*
  Conidiophores very toruloid at tip ..... *H. guareicolum*
Conidia not often more than 3-septate
  Conidiophores pale, translucent ..... *H. ocoteae*
  Conidiophores not pale and translucent
    Conidia usually not strongly differentiated at two ends
      Conidiophores 280 μ ..... *H. melastomacearum*
      Conidiophores 170 μ ..... *H. panici*
    Conidia differentiated strongly at two ends
      Beak short, usually 7 μ ..... *H. parathesicolum*
      Beak longer, usually 7 μ or more
        Conidiophores thick, 7 μ ..... *H. helleri*
        Conidiophores thin, 4 μ ..... *H. philodendri*

Helminthosporium glabroides, sp. nov. (figs. 8–10).—Mycelium very fine, pale, almost hyaline, conidiophores solitary, but often close together, about 100–140×7 μ, dark, sometimes pale at apex, often bent but not toruloid. Conidia 3–6-septate, 40–81×6–7 μ, truncate at base, tapering at apex.

On *Meliola glabroides* Stev. on *Piper aduncum*, 9039, El Alto de la Bandera (type), 4390, Lares, 3582, Añasco, 3647, Maricao, 4802, 3371, 7297, Arecibo, 8471, Aibonito, 9603, Las Marias. The long conidia on this host are quite typical, with a truncate base and gradually tapering toward the apical end. Occasionally smaller, 3-septate spores are seen. These are shorter, proportionately thicker, and have a long apical cell. The variation from the long, many-celled spore to the shorter 3-celled one is sometimes striking. In one part of the microscope field one form may predominate, while in another part of this field the other spore form is dominant.

On *Meliola comocladiae* Stev. on *Comocladia glabra*, 7484, 7056, Mayaguez, 760, Maricao. The conidiophores are darker than in the type and are sometimes slightly toruloid. Occasionally there is a strong tendency for them to be in groups.

On *Meliola hessii* Stev. on *Paullinia pinnata*, 1207b, Mayaguez. On *Meliola didymopanicis* P. Henn. on *Dendropanax arboreum*, 7440. On *Meliola polytricha* K. and C. no. 1256 (type specimen loaned from the Kew collection). No "conidial stage" was described for this by GAILLARD, although the type specimen contains abundant conidia, and these are mentioned by the authors of the species.

On *Meliola laguncularíae* E. on *Conocarpus erecta* L., 9201, Guanajibo. On *Meliola longipoda* Gaill. on *Tournefortia hirsutissima*, 7965, near Utuado. On *Meliola gesneriae* Stev. on *Cestrum laurifolium*, 824, Maricao. On *Meliola maricaensis* Stev. on *Ilex nitida*, 3679, 3607, Maricao. On *Meliola compositarum* var. *portoricensis*. Stev. on *Eupatorium portoricense*, 7320, Arecibo-Lares Road, 7723, Vega Baja, 6031, 6032, near Utuado; on *Eupatorium odoratum*, 6056, near Utuado. On *Meliola psychotriae* E. on *Chiococca alba*, 9299, Martin Peña, 7859, Rio Tanamá, 7467, Mayaguez. Conidia on this host are somewhat shorter than in the type. The conidiophores on no. 9299, and other specimens are sometimes quite strongly tufted, but they often grow singly as well.

On *Meliola puiggiarii* Speg. on Rubus, 8650, El Alto de la Bandera. On *Meliola gaillardiana* Stev. on *Piper aduncum*, 8225, Las Marias, 7796, Rio Arecibo. On *Meliola pteridicola* Stev. on *Aneimia adiantifolia*, 7814, Rio Tanamá, 7269, Quebradillas; on *Adiantum latifolium*, 8182, Las Marias, 7418, Mayaguez. On *Meliola toruloidea* Stev. on *Cassia quinquadrangulata*, 8394, Jajome Alto. On *Meliola monensis* Stev. on *Amyris elemifera*, 6150, Mona Island. On *Meliola nigra* Stev. on *Laguncularia racemosa*, 7197, Guanajibo.

This species is clearly differentiated from all other Porto Rican forms, and from all forms previously described associated with *Meliola*, by the long, narrow, many-septate conidia.

Helminthosporium guareicolum, sp. nov. (fig. 16).—Mycelium abundant, fine, pale. Conidiophores many, dark, basal part rigid, straight, upper part very torulose often for considerable distance (70 μ or more). Conidia truncate at base, beaked at apex, 3 or more septate.

On *M. guareicola* Stev. on *Guarea trichilioides*, 8166, Las Marias (type) 8096, Utuado.

Helminthosporium ocoteae, sp. nov.—Mycelium fine, pale straw color, diffuse. Conidiophores pale straw color, translucent, septate, tips crooked, 135–200×4 μ. Conidia 3-septate, 20–28× 4–6 μ.

On *Meliola ocoteae* Stev. on *Ocotea leucoxylon*, 8428, Jajome Alto (type).

The distinguishing character of this species is in the pale, translucent conidiophores.

Helminthosporium melastomacearum, sp. nov. (fig. 11).—Mycelium very fine, 1–1.5 μ, reticulated. Conidiophores abundant, black, lax, long, thin, 280×3 μ. Conidia narrowly elliptical, 3-septate, acute at each end, 14–21×3.5–6 μ.

On *Meliola melastomacearum* Speg. on *Miconia racemosa*, 7380, Mayaguez (type). On *Meliola glabra* var. *psychotriae* Stev. on *Psychotria grandis*, 7487, Mayaguez. On *Meliola paulliniae* Stev. on *Cascaria arborea*, 5709, Monte de Oro; on *Cascaria sylvestris*, 1051, Mayaguez, 7285, Arecibo-Lares Road.

Helminthosporium panici, sp. nov.—Mycelium fine, pale, in loose network. Conidiophores 170×4 μ, dark, pale at tip. Conidia 3-septate, terminal cells usually pale, central cells darker, basal cell truncate, apical cell constituting a short beak.

On *Meliola panici* E. on *Olyra latifolia*, 9159 (type), 7390, Mayaguez. On *Meliola rectangularis* Stev. on *Coccoloba laurifolia*, 7202, Arecibo-Lares Road.

Helminthosporium parathesicolum, sp. nov. (fig. 12).—Mycelium copious, fine, 1.5 μ. Conidiophores solitary, pale, 120×4 μ. Conidia 1–3-septate, 17–20×4–6 μ, base truncate, apex beaked, beak often 7 μ long.

On *Meliola parathesicola* Stev. on *Parathesis serrulata*, 8192, Las Marias (type), 7286, Arecibo-Lares Road. On *Meliola bicornis* Wint. on *Dalbergia monetaria*, Arecibo-Lares Road, 7243. On *Meliola rectangularis* Stev. on *Banisteria laurifolia*, 4392, 4384, Utuado, 7358, Hormigueros, 7564, Mayaguez.

This species is similar to *H. panici*, but is distinguished from it by the beaked conidia. It appears to be identical with the structures described as conidia of *M. bicornis* by GAILLARD, although the conidia here are somewhat smaller.

Helminthosporium philodendri, sp. nov. (fig. 13).—Mycelium fine, pale. Conidiophores abundant, long, slender, 400×3–4 μ, torulose at tip. Conidia 3-septate when mature, clavate, distinctly beaked, 24–35×5–8 μ.

On *Meliola philodendri* Stev. on *Philodendrum krebsii*, 4346, Ponce.

Helminthosporium helleri, sp. nov. (figs. 14, 15).—Mycelium fine. Conidiophores solitary, black, 230×7 μ. Conidia 3-septate when mature, clavate, 24–35×5–9 μ, well differentiated basal and apical cells.

On *Meliola helleri* E. on *Myrcia deflexa*, 8268 (type), 8296, El Alto de la Bandera; on *Eugenia stahlii*, 5343, Luquillo Forest, 8436, Jajome Alto. On

Meliola gaillardiana Stev. on *Piper aduncum*, 7794, Rio Arecibo. On *Meliola glabroides* Stev. on *Nectandra patens*, 8874, Maricao. On *Meliola thouiniae* on *Winterana canella*, 8548, 9075, Guayanilla. On *Meliola gymnanthicola* Stev. on *Gymnanthes lucida*, 8596, Guayanilla. On *Meliola toruloidea* Stev. on *Cassia quinquadrangulata*, 4015, Aibonito; on *Spondias mombin*, 749, Maricao. The short, plump, 3-septate conidia are often the most numerous types on this host. On *Meliola paulliniae* Stev. on *Paullinia pinnata*, 576, Vega Baja. On *Meliola myrsinacearum* Stev. on *Ardisia guadalupensis*, 7576, 7057, Mayaguez, 3681, 8005, Maricao. The form described as conidia of *M. pulveracea* perhaps belongs here. On *Meliola guignardi* Gaill. on *Turpinia panniculata*, 3635, Maricao. On *Meliola dipholidis* Stev. on *Dipholis salicifolia*, 8549, Guayanilla. On *Meliola monensis* Stev. on *Amyris elemifera*, 6150, Mona Island. On *Meliola furcata* Lev. on *Thrinax ponceana*, 8500, 8017, Guayanilla. This last number often shows large variation in size of spores, some being very small. On *Meliola guareae* Speg. on *Guarea trichilioides*, 7464, Mayaguez. I would place here also the forms described as conidia of *M. palmicola* Gaillard, also perhaps those of *M. patouillardi*.

Species indeterminate.—On *Meliola mayaguesiana* Stev. on *Palicourea crocea*, 7196, Lajas. Mycelium very scant, conidiophores few and scattered. Conidia not seen.

In addition to the species mentioned, other species which have been recorded on *Meliola* are *H. podosporiopsis* Pat. and *H. argentinum* Speg., both of which are 4-septate; the first on unknown host, the latter on *M. argentina* and *M. uvariae*.

Species of *Helminthosporium* which do not agree with any yet mentioned have been described as conidial stages of the following: *M. manosensis*, *M. martiniana*, *M. evodiae*, *M. hyalospora*, *M. quercinopsis*.

Sterile mycelium, probably that of *Helminthosporium*, has been recorded on *M. tomentosa*, *M. lanosa*, *M. clandestina*, *M. zig-zag*.

The "conidial stages" on *M. substenospora*, *M. quericina*, *M. anomala*, *M. butleri*, *M. pulveracea*, *M. iquitosensis*, *M. psidii*, *M. monilispora*, have been so briefly described that they are not recognizable.

On the following species of *Meliola* the species of *Helminthosporium* are perhaps distinct from those already mentioned: *M. wrightii*, *M. cryptocarpa*, *M. mitchellae*.

Isthmospora, gen. nov.—Mycelium and conidiophores dark. Conidia consisting of two approximately equal halves connected by a narrow isthmus, dark. The type of the genus is *I. spinosa.*

The species here characterized are of very unique form. They clearly belong to the Fungi Imperfecti, Dematiaceae, and in this family can only find kinship in that heterogeneous group the Staurosporae, among which, however, there is no genus closely related to the present forms. They differ from *Desmidiospora*, which has two conidial forms and a hyaline mycelium, in the absence of both of these characters. There is some resemblance to *Spegazzinia* and *Tetracoccosporium*, which have been placed in the Tuberculariaceae. The difference in spore structure, however, is sufficient to separate the genus *Isthmospora* from both of these.

Isthmospora spinosa, sp. nov. (fig. 17).—Mycelium fine, 1–2 μ, pale brown, aggregated into dense knots enveloping parts of the host mycelium. Conidiophores short, but slightly differentiated from the mycelium. The spores viewed from above are seen to consist of 4 major cells which are dark colored and rather thickly set with spines, each spine about 1 μ long. The major cells are arranged in two pairs which are connected by a 2-celled isthmus. This isthmus is flanked on either side by a circular, hyaline cell. Dimensions: total length 17–24 μ, breadth 14–20 μ, isthmus 3–4 μ wide, hyaline cell 3–4 μ in diameter.

On *Meliola psidii* Fr. on *Psidium guajava*, 3120 (type), Yauco, 5642a, Jajome Alto. On *Meliola chiococcae* Stev. on *Chiococca alba*, 7743, Vega Baja. On *Meliola byrsonimae* Stev. on *Byrsonima lucida*, 3541, Guayanilla. On *Meliola smilacis* Stev. on *Smilax coriaceae*, 5261, Manati. On *Meliola helleri* E. on *Myrcia splendens*, 5646, Jajome Alto. On *Meliola praetervisa* Gaill. on *Coccolobis sintenisii*, 7066, Mayaguez, and on *Coccolobis pyrifolia*, 7065, Mayaguez. On *Meliola philodendri* Stev. on *Philodendron krebsii*, 7225, Arecibo-Lares Road, 8994, Maricao, 4346, Ponce, 8712, El Alto de la Bandera.

Isthmospora glabra, sp. nov. (fig. 18).—Mycelium fine, 1–2 μ, pale, aggregated into knots on the host mycelium. Conidiophores short, slightly different from the mycelium. Spores of 4 major cells in 2 pairs connected by an isthmus; isthmus dark, major cells pale straw to wine colored, glabrous; total dimensions 9×10 μ.

On *Meliola melastomacearum* Speg. on *Clidemia hirta*, 9479, near Utuado. On *Meliola psychotriae* E. on *Gonzalagunia spicata*, 7793, Rio Arecibo, 7044, 7046, Mayaguez. On *Meliola bicornis* Wint. on *Meibomia supina*, 8075, Maricao. On *Meliola glabroides* Stev. on *Nectandra patens*, 8973, Maricao, and on

Simaruba tulae, 7588, Mayaguez. On *Meliola glabra* B. and C. (Rabenhorst. Fungi Europaei, no. 3849).

This species is clearly separated from the last by its small, irregular, pale spores, but most strikingly by the absence of spines which are so conspicuous on *I. spinosa*.

While the species have been seen only upon the recorded hosts, they may well occur upon others, since when sparsely present they are easily overlooked.

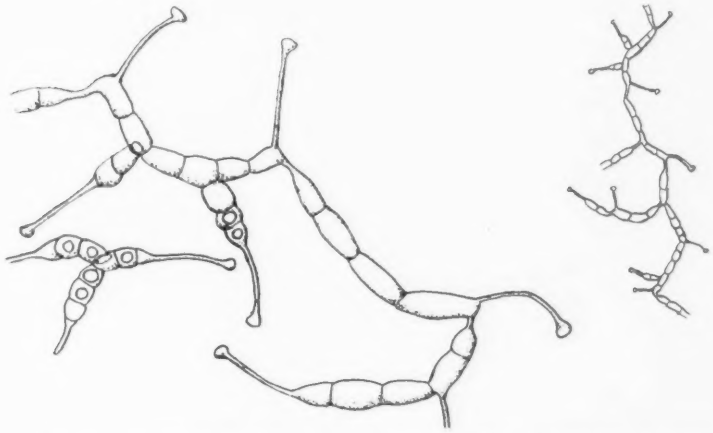


FIG. 5.—*Grallomyces portoricensis*, showing general habit of branching of mycelium and structure of supporting organs; on *Clusia minor*, no. 8283 (type) *l.p.* and *h.p.*

Fusarium meliolicolum, sp. nov.—Mycelium indistinguishable from that of *Nectria meliolicola*. Conidiophores short, cespitose in small sporodochia, 50–60 μ in diameter or by coalesence larger. Conidia clavate, curved, apex obtuse, base attenuate, 16–19 × 2.5 μ, 1–3-septate. Associated with and probably the conidial form of *Nectria meliolicola*.

On *Meliola paullíniae* on *Cascaria sylvestris*, 1051, Mayaguez (type).

Grallomyces, gen. nov.—Mycelium raised from the surface by supports (*grallae*, stilts).

Grallomyces portoricensis, sp. nov. (text fig. 5).—Mycelium composed of segments arranged in zigzag fashion, strongly

constricted between segments. Supports to mycelium 17–27 μ long, with disk-formed attachments at base.

On *Clusia minor*, 8283 (type), El Alto de la Bandera; on *Guarea trichilioides*, 8166, Las Marias; on *Cascaria* sp., 7074, Mayaguez; on *Mammea americana*, 8207, Las Marias; on *Palicourea crocea*, 7196, Lajas; on *Scleria* spp., 5252, Manati; on *Eugenia stahlii*, 5343, Luquillo Forest; on *Nectandra patens*, 7081, Mayaguez; on (?), 4521; on *Myrcia* sp., 818, Maricao.

The mycelium is dark brown, with some cells pale brown to straw color. It may be described as consisting of links composed of usually 4 or 5 cells each. There is some constriction at the septa between cells. The links are arranged at angles, giving the whole mycelium a zigzag or "rail fence" appearance. Each end of each link is constricted to a short (3–7 μ), narrow (2–3 μ) isthmus which forms connection with the next link. This structure is in itself remarkable enough, but more remarkable is the fact that the whole mycelium is supported free from its underlying medium by a series of "stilts" which are about 17–27 μ long. These stilts are quite uniformly distributed, one at each constriction of the mycelium, and they appear to be a projection of the constricted portion, while the next link appears as a side growth from it. The stilts are terminated by a circular enlargement which is evidently a holdfast organ. No spores or conidiophores were seen.

This fungus is often associated with *Meliola* of various species, but seems to have no connection with them. It appears to have no definite hosts, but to grow on any leaf where suitable atmospheric conditions obtain.

The following fungi not already mentioned have also been reported upon *Meliola*: *Dimerosporium apertum*, *Dimerium guinier*, *Hyaloderma piliferum*, *H. subastomum*, *H. tricholomum*, *H. lateritium*, *Zukalia vagans*, *Pseudomeliola* (?) *collapsa*, *Melanopsamma parasitica*, *Acerbiella violacea*, *Nectria aureola*, *N. bakeri*, *Calonectria inconspicua*, *C. lagerheimiana*, *C. erysiphoides*, *Paranectria wildemaniana*, *Lochnospermella tetraspora*, *Monosporium meliolicola*, *Mycogone meliolarum*, *Helminthosporium podosporiopsis*, *Arthrosporium parasiticum*, *Isariopsis penicillata*, *Podosporium densum*, *P. penicillioides*, *P. penicillium*. *Spegazzinia meliolicola*, *S. meliolae*, *S. coffeae*.

ALPHABETICAL LIST OF MELIOLAS AND THE FUNGI FOUND UPON THEM

M. ambigua.—Arthrobotryum caudatum.
M. andirae.—Calonectria graminicola.
M. arecibensis.—Coniothyrium glabroides.

M. bicornis.—Dimerium piceum, Microthyriaceae indet., Calonectria melioloides, Arthrobotryum caudatum, Helminthosporium parathesicolum, Isthmospora glabra.
M. byrsonimae.—Isthmospora spinosa.
M. chiococcae.—Belonidium leucorrhodinum, Isthmospora spinosa.
M. comocladiae.—Helminthosporium glabroides.
M. compositarum.—Coniothyrium glabroides.
M. compositarum var. portoricensis.—Perisporium meliolae, Dimerium piceum, Calonectria melioloides, Coniothyrium glabroides, Helminthosporium glabroides.
M. cupaniae.—Calonectria melioloides.
M. didymopanicis.—Arthrobotryum caudatum, Helminthosporium glabroides.
M. dieffenbachiae.—Arthrobotryum dieffenbachiae.
M. dipholidis.—Helminthosporium helleri.
M. furcata.—Helminthosporium helleri.
M. gaillardiana.—Microthyriaceae indet., Helminthosporium glabroides, H. helleri.
M. gesneriae.—Helminthosporium glabroides.
M. glabra.—Isthmospora glabra.
M. glabra var. psychotriae.—Dimerium piceum, Microthyriaceae indet., Arthrobotryum caudatum, Helminthosporium melastomacearum.
M. glabroides.—Dimerium piceum, Microthyriaceae indet., Paranectria meliolicola, Coniothyrium glabroides, Arthrobotyrum glabroides, A. caudatum, Helminthosporium glabroides, H. helleri, Isthmospora glabra.
M. guareae.—Helminthosporium helleri.
M. guareicola.—Coniothyrium glabroides, Helminthosporium glabroides.
M. guignardi.—Helminthosporium helleri.
M. gymnanthicola.—Helminthosporium helleri.
M. helleri.—Microthyriaceae indet., Helminthosporium helleri, Isthmospora spinosa.
M. hessii.—Perisporium paulliniae, Calonectria melioloides, Helminthosporium glabroides.
M. hyptidicola.—Microthyriaceae indet., Naemosphaera hyptidicola, Arthrobotryum caudatum.
M. ipomoeae.—Dimerium piceum.
M. longipoda.—Microthyriaceae indet., Arthrobotryum caudatum, Helminthosporium glabroides.
M. maricaensis.—Helminthosporium glabroides.
M. mayaguesiana.—Helminthosporium helleri.
M. melastomacearum.—Microthyriaceae indet., Nectria portoricensis, Arthrobotryum caudatum, Helminthosporium ocoteae, Isthmospora glabra.
M. monensis.—Calonectria melioloides, Helminthosporium helleri.
M. myrsinacearum.—Helminthosporium helleri.

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M. gaillardiana.—Microthyriaceae indet., Helminthosporium glabroides, H. helleri.
M. gesneriae.—Helminthosporium glabroides.
M. glabra.—Isthmospora glabra.
M. glabra var. psychotriae.—Dimerium piceum, Microthyriaceae indet., Arthrobotryum caudatum, Helminthosporium melastomacearum.
M. glabroides.—Dimerium piceum, Microthyriaceae indet., Paranectria meliolicola, Coniothyrium glabroides, Arthrobotyrum glabroides, A. caudatum, Helminthosporium glabroides, H. helleri, Isthmospora glabra.
M. guareae.—Helminthosporium helleri.
M. guareicola.—Coniothyrium glabroides, Helminthosporium glabroides.
M. guignardi.—Helminthosporium helleri.
M. gymnanthicola.—Helminthosporium helleri.
M. helleri.—Microthyriaceae indet., Helminthosporium helleri, Isthmospora spinosa.
M. hessii.—Perisporium paulliniae, Calonectria melioloides, Helminthosporium glabroides.
M. hyptidicola.—Microthyriaceae indet., Naemosphaera hyptidicola, Arthrobotryum caudatum.
M. ipomoeae.—Dimerium piceum.
M. longipoda.—Microthyriaceae indet., Arthrobotryum caudatum, Helminthosporium glabroides.
M. maricaensis.—Helminthosporium glabroides.
M. mayaguesiana.—Helminthosporium helleri.
M. melastomacearum.—Microthyriaceae indet., Nectria portoricensis, Arthrobotryum caudatum, Helminthosporium ocoteae, Isthmospora glabra.
M. monensis.—Calonectria melioloides, Helminthosporium helleri.
M. myrsinacearum.—Helminthosporium helleri.

M. nigra.—Helminthosporium glabroides.
M. ocoteae.—Helminthosporium ocoteae.
M. panici.—Dimerium piceum, Calonectria graminicola, Coniothyrum glabroides, Arthrobotryum penicillium, Helminthosporium panici.
M. parathesicola.—Helminthosporium parathesicolum.
M. philodendri.—Helminthosporium philodendri, Isthmospora spinosa.
M. praetervisa.—Isthmospora spinosa.
M. paulliniae.—Dimerium piceum, Nectria meliolicola, Calonectria melioloides, Arthrobotryum caudatum, Helminthosporium melastomacearum, H. helleri, Fusarium meliolicolum.
M. psidii.—Isthmospora spinosa.
M. psychotriae.—Microthyriaceae indet., Arthrobotryum caudatum, Helminthosporium glabroides, Isthmospora glabra.
M. pteridicola.—Dimerium piceum, Microthyriaceae indet., Coniothyrium glabroides, Arthrobotryum caudatum, Helminthosporium glabroides.
M. puiggiarii.—Helminthosporium glabroides.
M. rectangularis.—Nectria portoricensis, Helminthosporium panici, H. parathesicolum.
M. rudolphiae.—Belonidium leucorrhodinum.
M. smilacis.—Isthmospora spinosa.
M. thouiniae.—Helminthosporium helleri.
M. tortuosa.—Belonidium leucorrhodinum, Dimerium piceum, Pseudonectria pipericola, Calonectria melioloides, Paranectria meliolicola, Coniothyrium glabroides.
M. toruloidea.—Calonectria graminicola, Helminthosporium glabroides, H. helleri.
M. triumfettae.—Microthyriaceae indet.
Microthyriaceous fungus.—Paranectria miconiae.

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EXPLANATION OF PLATES V AND VI

(*l.p.* indicates low power; *h.p.*, high power)

PLATE V

Arthrobotryum

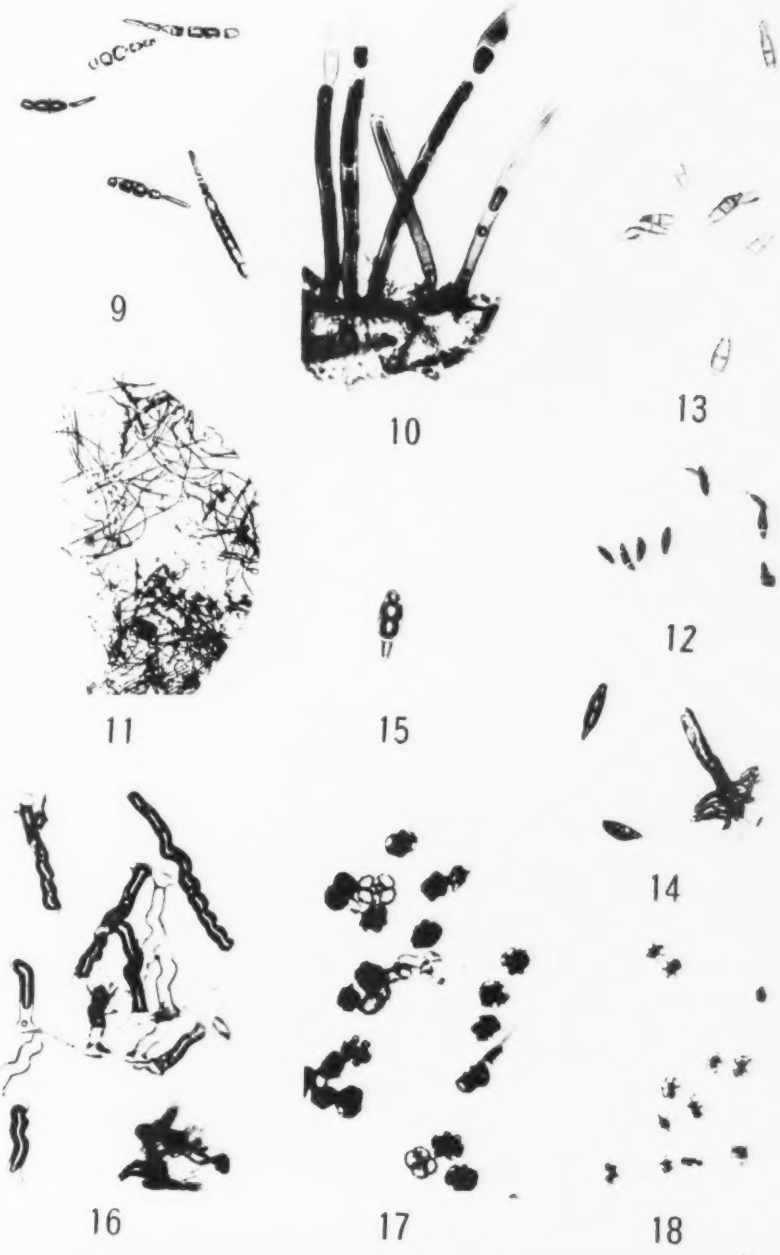
FIG. 1.—*A. glabroides:* fine mycelium overgrowing coarse mycelium of *Meliola;* 7595a, *l.p.*

FIG. 2.—Same, *h.p.*

FIG. 3.—Spores: 7595b, *h.p.*

FIG. 4.—*A. dieffenbachiae:* coremium on a seta; 8077, setal forkings are clearly shown in the coremium.

STEVENS on MELIOLA PARASITES



STEVENS on MELIOLA PARASITES

FIG. 5.—*A. caudatum*, showing coremia; *l.p.*

FIG. 6.—*A. caudatum*, showing 2 kinds of mycelium and spores; 7745.

FIG. 7.—*A. caudatum*, showing coremia; 468, *l.p.*

Helminthosporium

FIG. 8.—*H. glabroides* on *Meliola polytricha:* conidia; 1256, Kew Botanical Gardens, *h.p.*

PLATE VI

FIG. 9.—*H. glabroides:* typical long and short spores; 9039, *h.p.*

FIG. 10.—*H. glabroides* on *M. longipoda:* conidia on conidiophores, showing that truncate end is basal; 7965, *h.p.*

FIG. 11.—*H. melastomaceaum* on *M. melastomaceaum:* conidia and conidiophores; 7389, *l.p.*

FIG. 12.—*H. parathesicolum* on *M. parathesicola:* spores; 8192, *h.p.*

FIG. 13.—*H. philodendri* on *M. philodendri:* spores; 4346, *h.p.*

FIG. 14.—*H. helleri* on *M. helleri:* spores and a conidiophore showing its mycelium; 8268, *h.p.*

FIG. 15.—*H. helleri* on *M. guignardia:* spore; 3635, *h.p.*

FIG. 16.—*H. guareicolum* on *M. guareicola:* 8166, *h.p.*, showing toruloid conidiophores.

Isthmospora

FIG. 17.—*I. spinosa:* spores; 3120, *h.p.*

FIG. 18.—*I. glabra:* spores; 9479, *h.p.*

ANATOMY OF CERTAIN GOLDENRODS[1]

EDITH S. WHITAKER

(WITH PLATES VII AND VIII AND ONE FIGURE)

In dealing with the anatomical features of *Solidago*, and especially in studying the modifications of its woody cylinder in relation to the leaf trace, it is well to bear in mind the fact that the goldenrods belong to a family which occupies a high place systematically. The largest proportion of herbs and short-lived perennials, especially in temperate regions, belongs to the Compositae; and since they are so generally admitted to be high forms, a certain amount of evolutionary progress can be taken for granted in studying them. Another advantage in investigating genera of the Compositae is the fact that in the family and in any genus of the family both the woody and herbaceous type of stem may be found; hence comparisons are more easily made and conclusions more readily drawn. Not only within the same genus are both kinds of stem to be found, but the same aerial axis has regions which are characteristically woody and herbaceous. This situation is well illustrated by *Solidago*. In the lower portions of the aerial axis, as well as in the subterranean parts of the stem, the organization is typically woody; while in the higher and more slender portions of the stem the herbaceous type prevails. In short, *Solidago* presents an epitome of a woody-herbaceous condition in which the transition from one type to the other is advantageously elucidated.

The species of goldenrod studied were *Solidago canadensis*, *S. bicolor*, *S. rigida*, *S. caesia*, *S. speciosa*, *S. sempervirens*, *S. graminifolia*, *S. latifolia*, *S. serotina*, and *S. patula*. It was found that in all these species there are certain modifications of the woody cylinder related definitely to the leaf strands. These consist in the transformation of portions of the woody segment through which the leaf trace takes its departure into parenchyma and in the elimination of fibers and vessels.

[1] Contributions from the Laboratories of Plant Morphology of Harvard University.

There are, as a rule, three traces to each leaf in *Solidago*, a median and two laterals. In some species (for example, *S. rigida*, *S. patula*, and *S. sempervirens*) there is a multiplication of traces, correlated apparently with the increased size and vigor of the plants and especially with the size of their leaves. The species mentioned, besides being very large and leafy, are characterized by having large, full heads of flowers.

In studying the modifications of the woody cylinder, the median trace need not be especially considered, since conditions here are complicated by the presence of the axillary bud. Attention accordingly may be directed to the lateral traces, which present a simpler situation. The most conservative part of the stem is at the node; and conditions at the node, therefore, are the most significant. A section cut transversely through the node of the woody axis of any of the species of *Solidago* mentioned shows the leaf traces still in the cortex. Following the traces down in serial sections, it is to be noted that they enter the woody cylinder a short distance below the node and are surrounded on all sides by parenchyma. One leaf trace usually passes into the stele at a higher level than the others. Consequently, sections cut at different distances below the node show the traces in different topographical relations. For a considerable interval downward the trace is surrounded on all sides by parenchyma, so that the storage elements are present not only on the sides of the trace but confront it externally as well.

Fig. 1 shows a transverse section of *S. canadensis* cut far enough below the node so that only one of the lateral traces (the one on the right which entered the cylinder much lower than the corresponding trace on the left) appears surrounded on all sides by parenchyma. Figs. 2, 3, and 4 show this situation under higher degrees of magnification and in the three dimensions respectively. Fig. 2 is a high power representation of the transverse section of a lateral leaf trace segment of *S. canadensis*. The foliar strand can be seen lying at the bottom of the figure, obviously surrounded by storage parenchyma, which both confronts it radially and lies on either side of it. In this section it is clear that a portion of the cylinder opposite the leaf trace has undergone considerable modification, apparently in relation to the photosynthetic activity of the leaf. The cauline

segment in relation to it may conveniently be designated as the leaf trace segment. Fig. 3 shows the same situation in longitudinal tangential aspect. Here the trace appears high up in the center of the figure and is obviously surrounded on all sides by parenchymatous tissue. This section was made near the region of the cortex, so that it represents the leaf strand after it has become horizontally inclined. Fig. 4 is a radial view of the same situation, illustrating in a similar manner the imbedding of the leaf trace in storage tissue in its course through the woody cylinder. This section also demonstrates the fact that vessels and fibers again make their appearance in the cylinder directly above the leaf trace segment after the foliar strand has passed into the cortex.

It is clear from the foregoing illustrations that the woody cylinder opposite the leaf trace undergoes certain modifications in relation to the activity of the foliar organ. The strand as it passes upward and outward through the cylinder is flanked on either hand by storage tissue which may be designated as flanking parenchyma. Farther in its outward course, and more marked where the cylinder is thick, subtending the trace externally is a mass of tissue which may appropriately be called subtending or confronting parenchyma. Above the trace is the parenchymatous interval known as the leaf gap. It is noteworthy in this connection that the leaf trace in the thick or woody cylinder (and all the axes here figured are aerial) of *S. canadensis* has the same topographical relation to storage devices as is found in arboreal types like *Quercus*, *Casuarina*, etc. The origin and topographical relations of the broad ray in the oak have clearly and convincingly been elucidated by EAMES,[2] and the conclusions reached by this author have been shown by BAILEY[3] to hold with equal validity for the Betulaceae and Fagaceae in general. EAMES[4] has also shown that the woody type in the Rosaceae is subject to the same general modifications in relation to the leaf trace as obtained in the Betulaceae, Fagaceae, and also,

[2] EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. **49**: 161–167. 1910.

[3] BAILEY, I. W., Relation of leaf-trace to compound rays in lower dicotyledons. Ann. Botany **25**: 225–241. *pls. 15–17. fig. 1.* 1911.

[4] EAMES, A. J., Herbaceous type in angiosperms. Ann. Botany **25**: 215–224. *pl. 14.* 1911.

as has been shown, in the woody aerial stem of *Solidago*. It is clear that there is a general agreement regarding the part the leaf trace plays in relation to the transformation of portions of the woody cylinder into a parenchymatous segment.

Concerning the comparableness of woody types like the oak, etc., with those presented by axes characteristically herbaceous, however, some doubts have been raised. It has, for instance, been maintained by SINNOTT and BAILEY[5] that the herbaceous type does not come from the woody through the conversion of secondary xylem opposite the leaf strand into storage parenchyma, but, on the contrary, that the evolution of herbaceous forms has come about through the reduction in amount of secondary wood and increase in width of the broad rays. This, together with their decrease in radial extent, has resulted in the confining of the storage tissue in herbaceous axes to the sides of the leaf trace, with the result that parenchyma in no case subtends the trace as in the oak, etc. "In practically all families of herbs, the interfascicular parenchyma is never subtended by a tiny leaf trace bundle of protoxylem, but always abuts directly on the pith tissue between the strands of primary wood" (*loc. cit.* p. 596). Hence it is assumed that the significant conditions in the woody stem in relation to the leaf trace are in no way responsible for the origin of the herbaceous form. It is further claimed, in substantiation of this hypothesis, that the condition outlined for the Betulaceae, etc., while it holds for the subterranean parts of the woody axis, does not explain the situation in the aerial region of the herbaceous stem where "the actual evolutionary development must have taken place (*loc. cit.* p. 555).

The situation in the herbaceous part of *Solidago* may be described. Fig. 5 represents a slender stem of *S. canadensis*, which is obviously herbaceous. The section was made just below the node and shows the three leaf traces at the top. At the bottom and a little to the right, the three traces of the next higher node may be seen. In the upper part of the figure, even under the comparatively low power of magnification, it can easily be noted that the

[5] SINNOTT, E. W., and BAILEY, I. W., Investigations on the phylogeny of the angiosperms. IV. The origin and dispersal of herbaceous angiosperms. Ann. Botany **28**:547–600. *pls. 39, 40.* 1914.

traces pass out surrounded by parenchyma. Fig. 6 is a more highly magnified view of one of the lateral leaf traces, showing that even in the upper aerial region of this persistently woody species confronting as well as flanking parenchyma is present. Fig. 6 also elucidates the relatively greater size of the leaf trace in proportion to the segment, as compared with fig. 2. Allowing for the difference in the size of the leaf trace and for the inevitable thinning of the cylinder in the more slender portions of this particular stem, as well as in herbaceous forms generally, one can readily see how, if the cylinder were sufficiently reduced in size, the subtending storage tissue would be confined to the sides of the foliar strand even in the region of the node. Lower in the internode there would normally be only flanking parenchyma, since the central region of the confronting parenchyma is transformed below into a characteristically woody segment composed of vessels, fibers, etc. EAMES (*loc. cit.*) has made it clear that in the Rosaceae in which both woody and herbaceous types occur the latter has undoubtedly come from the former by the parenchymatous transformation of more and more secondary wood in proximity to the leaf traces. Hence the bundles of the herbaceous stem represent ordinary woody segments interspersed with other segments which have undergone the parenchymatous metamorphosis described.

It would seem fairly clear from the preceding descriptions that the highest dicotyledons present the same general conditions of modification of the originally woody cylinder in relation to storage and the leaf trace as is found in the lower groups, such as the Betulaceae, Fagaceae, etc. It is quite clear that the herbaceous type has originated in a similar manner and largely as the result of the thinning of the woody cylinder. *Solidago* obviously illustrates this transition stage, since it shows in its herbaceous regions the same topographical relation to the cylinder as is found in the typically woody part of the axis. To elucidate this point, and chiefly for the sake of making the situation indubitably clear, the accompanying diagrams have been introduced.

In text fig. 1, *A* represents the woody portion of *Solidago*, and would also hold equally well for the woody dicotyledons with large foliar rays. On the other hand, *B* elucidates the characteristic

herbaceous condition in a dicotyledonous stem. In *A* the condition presented by figs. 2, 3, 4, and 6 is illustrated. The departing leaf traces in the region of the node, especially as they bend outward through the cylinder, are both flanked and subtended by storage parenchyma, a situation shown diagrammatically in black. *B* illustrates the topography of the herbaceous region of the stem in the Compositae, where, by reason of the greater relative importance of the leaf trace, its radial diameter nearly equals that of the ordinary xylem segments of the cylinder. As a consequence, the confronting parenchyma of *A* is conspicuously absent and the storage

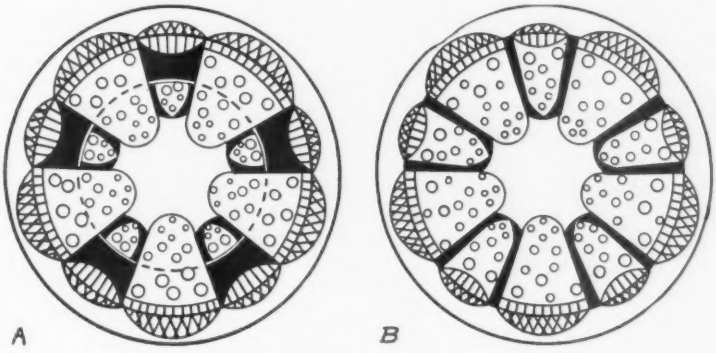


FIG. 1

tissue, as a necessary geometrical result, is confined to the flanks of the narrower segments representing the foliar strands. This exaggeration of the leaf trace in the herbaceous type is probably in response to the greater relative size and importance of the leaves. That the situation outlined in *B* obviously results from the thinning of the cylinder, with the consequent confining of the storage tissue exclusively to the sides of the trace, will be evident by referring to *A* and supposing the woody cylinder here to be considerably reduced in thickness. This hypothetical thinning of the cylinder is represented by a broken line drawn through the stele just outside the leaf traces. A comparison of the portion of the cylinder thus limited in *A* with the herbaceous type represented in *B* shows that the conditions inside the broken line are substantially the same as

those depicted in the latter illustration. The parenchyma in both is flanking only and the leaf trace plays a predominant part.

Hence, from a consideration of the situation obtaining from the lower dicotyledons to the Compositae, it would seem clear that the herbaceous type has been derived from the woody through the conversion of segments related to the outgoing leaf strand into wood parenchyma; and that in extreme herbaceous types the storage tissue has become confined to the sides of the trace by the simple process of the thinning of the cylinder and the increased relative importance of the foliar strand.

An interesting feature of some species of *Solidago* is the multiplication of leaf traces, a situation which might be expected in relation to the increased efficiency of the leaves. As has been stated, the usual number of traces in this genus is 3; but in more vigorous stems the leaf traces may be more numerous. In *S. patula*, for instance, there are 5; and in *S. sempervirens*, the salt marsh goldenrod, there are as many as 7 or 9, according to the vigor of the plant. This condition is represented in fig. 7, which is a transverse section of *S. sempervirens*. In the instances where there is a multiplication of leaf traces, it is noteworthy that in addition to stout and leafy stems, these species are likewise characterized by unusually large and full heads of flowers.

Another point of interest, which is of course a common anatomical characteristic of the Tubuliflorae, is the presence of oil canals in the pith or cortex, or in both. In fig. 7, which is a cross-section of *S. sempervirens*, these oil canals may easily be noted in both pith and cortex; and in fig. 5, which represents the same plane in *S. canadensis*, they are visible in the cortex only.

An additional feature of interest is presented by the leaf bundles in the cortex, namely, the presence of internal phloem. This is shown in fig. 8, which is a high magnification of one of the cortical bundles of *S. sempervirens*. Other species of *Solidago*, for example, *S. canadensis*, *S. patula*, *S. rigida*, etc., show the same organization of their cortical bundles, and it seems to be a general condition for the genus. It has been suggested by WORSDELL[6] in the case of the Cucurbitaceae that internal phloem is a "vestigial structure." In

[6] WORSDELL, W. C., The origin of medullary (interxylary) phloem in the stems of dicotyledons. Ann. Botany **29**: 567–590. *figs.* 10. 1915.

this family (the Cucurbitaceae), as is well known, the stem bundles are characterized by the presence of internal phloem. The conclusion has been reached by this author, as a result of the study of the conservative regions, that the internal phloem is derived from inversely oriented medullary bundles fused with the inner surface of the woody cylinder. The situation in *Solidago* (and in other genera of the Compositae) is of interest in this connection, especially as the presence of internal phloem is so constant a feature of the organization of the leaf trace in its course through the cortex. Since the results of comparative anatomical study of existing and extinct gymnosperms show clearly the conservative character of the leaf trace, it seems fairly obvious that the Compositae once possessed internal phloem in the stem like the Cucurbitaceae, Solanaceae, etc., but have lost it as a result of subsequent modifications. It may be pointed out that this assumption accords with the high systematic position ordinarily assigned to the family. This conclusion is in no way weakened by the fact that the Compositae are actually included in the same large group or cohort as the Cucurbitaceae, namely, the Campanulales (Campanulatae).

In *Solidago* and most genera of the Compositae there are depressions in the woody cylinder corresponding to the leaf trace segments. Work carried on in this laboratory by Mr. J. P. POOLE on *Helianthus* has demonstrated that in this genus the depressions invariably correspond to the foliar segment. Fig. 9, which is a woody stem of *H. hirsutus*, is inserted here because it illustrates this situation so diagrammatically. At either side two median traces are to be seen, and also their two corresponding lateral traces, making in all 6 depressions in the cylinder and 6 corresponding parenchymatous modifications. Most species of *Solidago* show similar depressions in immediate relation to the foliar segment. BAILEY[7] has made it clear that in the oak these depressed segments are caused by the retarding influence on growth of pairs of closely approximated compound foliar rays. The depressions in the Compositae in relation to the leaf trace segments are likewise connected with growth mechanics.

[7] BAILEY, I. W., The evolutionary history of the foliar ray. Ann. Botany **26**:647–661. *pls. 62–63*. 1911.

The situation in the oak, however, is somewhat different from that outlined for *Helianthus* and the Compositae generally; for in the oak the depressions are xylem segments *between* the lateral compound leaf rays and do not correspond to the leaf trace segment itself as in the Compositae. For purposes of elucidation the situation presented by the oaks may be briefly reviewed. In *Quercus* the two predominant lateral traces of each foliar organ are related to foliar rays which are typically in 5 pairs, corresponding to the two-fifths phyllotaxy of the oak. Between these approximated pairs of rays there is a "dipping in" of the cylinder as a consequence of the retarding influence on growth of the rays in question.

In some genera of the Compositae we get a situation approximating that in the oaks, and as a result contrasting with that figured for the sunflower, etc., in fig. 9. In *S. graminifolia*, for instance, the depressions do not correspond to single leaf trace segments as is usual in the Compositae, but are in relation to the xylem segments between the leaf rays. This situation may be noted in fig. 10, a section of *S. graminifolia* cut in the region of the node. The result of the depression of segments between the rays is that the stem is roughly divided into 5 parts as in the oak. The pith is 5-angled and the median trace comes off opposite an angle of the pith precisely as in *Quercus*. Fig. 11 shows a portion of the same more highly magnified, illustrating how striking is the depression and how clear the analogy to the oak. Fig. 12, which at first sight might easily be taken for a section of an oak twig, is really a transverse section of *Aster multiflorus*, and elucidates this phenomenon even more strikingly. Here there can be no doubt that the depressions in the cylinder occur between pairs of rays exactly as in *Quercus*, and do not correspond to single leaf trace segments. This topographical condition of the stem is rare in the Compositae, although it is occasionally present in *Solidago*, as for example in *S. graminifolia*, and is extremely common in the genus *Aster*.

Summary and conclusion

Solidago is a genus which occupies a very high place systematically and presents both woody and herbaceous types of stem, not only in the genus but also in different regions of the axis of the same species. The modifications of the stem, especially the transition

from one type to the other, therefore, can be studied to good advantage in this and other genera of the Compositae.

In connection with the derivation of the herbaceous type it has been shown that the general principles derived from the study of the Betulaceae, Fagaceae, Rosaceae, etc., hold equally well for this particular genus of the Compositae. Here as there the same storage modifications result from the transformation of woody tissues surrounding the outgoing leaf traces. No vessels appear in the leaf trace segment in the region just below the node, but at a lower level in the internode the foliar segment again becomes woody with typical vessels and fibers.

In the slender herbaceous part of the aerial axis the same general situation obtains. The traces, however, are relatively well developed in proportion to the size of the segment, and the cylinder as a whole is thinner. This thinning of the cylinder automatically results in the limiting of the storage elements to the flanks of the foliar strands in extreme herbs.

It seems noteworthy that in some species of *Solidago*, for example, in *S. sempervirens*, but occurring also in other species, there is a multiplication of the foliar traces which seems to be definitely correlated on the one hand with greater vegetative vigor and on the other hand with more numerous and larger heads of flowers.

Internal phloem in the leaf bundles of the cortex is a general feature of the genus and probably of the family. It seemingly perpetuates a condition which was once characteristic of the bundles of the axis.

Solidago occasionally resembles the oak anatomically by the "dipping in" of woody segments between the leaf rays in contrast to depressions in the cylinder corresponding to single leaf trace segments, as in *Helianthus* and the Compositae generally. The depression of the cylinder between leaf rays is the usual situation in the genus *Aster*, which, with certain species of *Solidago*, are exceptions to the general rule for the Compositae.

In conclusion I wish to thank Dr. E. C. JEFFREY, under whose direction this investigation has been carried on, for material, valuable advice, and suggestions.

HARVARD UNIVERSITY

EXPLANATION OF PLATES VII AND VIII

FIG. 1.—Transverse section of woody stem of *Solidago canadensis;* ×10.

FIG. 2.—Lateral leaf trace segment of same more highly magnified; ×50.

FIG. 3.—Tangential view of same; ×60.

FIG. 4.—Radial view of same; ×60.

FIG. 5.—Transverse section of upper and more herbaceous region of *S. canadensis;* ×15.

FIG. 6.—Lateral leaf trace segment of same more highly magnified; ×120.

FIG. 7.—Transverse view of section of *S. sempervirens* showing multiplication of leaf traces; ×12.

FIG. 8.—Leaf trace bundle of same section more highly magnified; ×150.

FIG. 9.—Transverse section of woody stem of *Helianthus hirsutus;* ×10.

FIG. 10.—Transverse section of *S. graminifolia;* ×8.

FIG. 11.—Part of thinner cylinder of same species more highly magnified; ×40.

FIG. 12.—Transverse view of section of *Aster multiflorus;* ×12.

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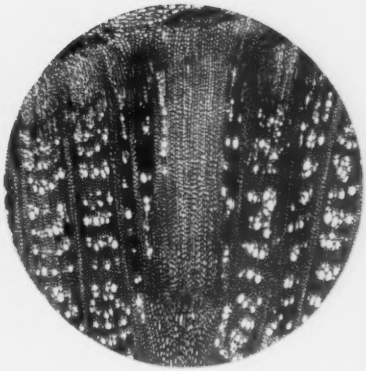

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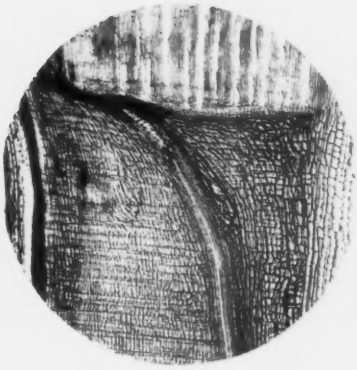

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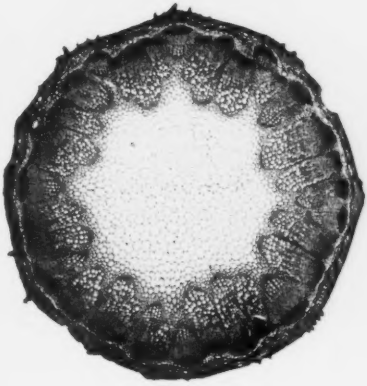

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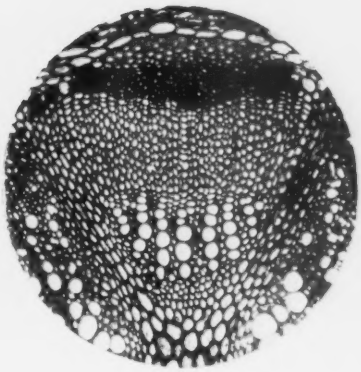
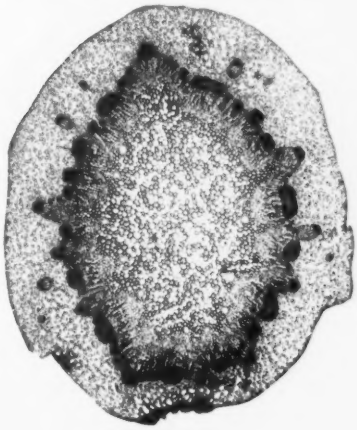


6

WHITAKER on SOLIDAGO



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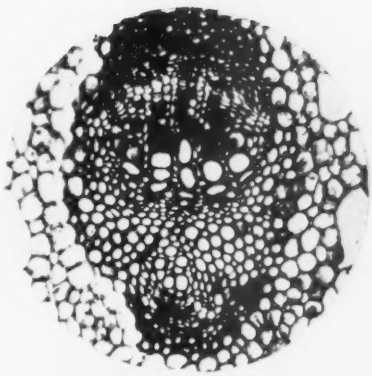

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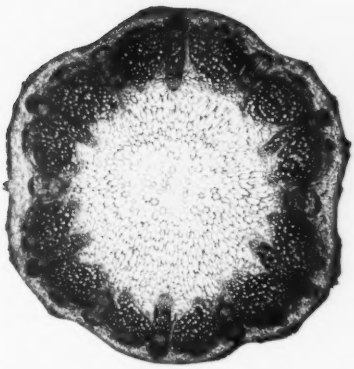

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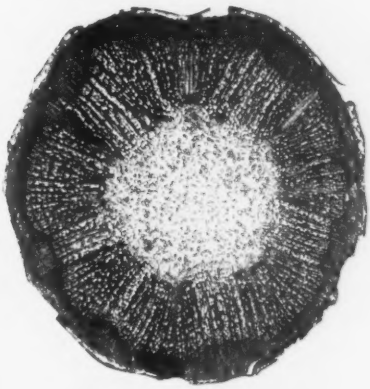

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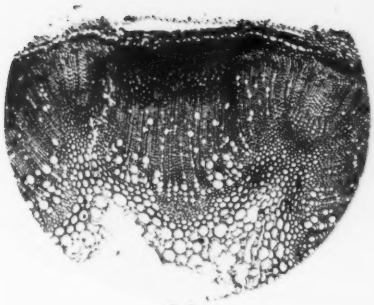

11

12

WHITAKER on SOLIDAGO

PELEA AND PLATYDESMA

JOSEPH F. ROCK

(WITH ONE FIGURE)

The family Rutaceae is represented in the Hawaiian Islands by several genera, of which the genus *Pelea*, named by ASA GRAY after the Hawaiian goddess of fire Pele, is the largest. The species, which number about 30, including the two here described, are more or less in a state of confusion. They are very difficult to separate, owing to the many varieties and intermediate forms. The writer was privileged to work for about three months at the Berlin Herbarium on the HILLEBRAND collection, shortly before the outbreak of the present war, and also at the Gray Herbarium, which enabled him to unravel some of the existing confusion. The present paper places a few species of *Pelea* in their proper positions and also clears up the synonymy of *P. auriculaefolia* Gray. Owing to HILLEBRAND'S misidentification of *P. kauaiensis*, HELLER, evidently relying on HILLEBRAND'S description of that species, described the true *P. kauaiensis* Mann as a new species, namely, *P. cruciata*, which must now remain a synonym.

PELEA SAPOTAEFOLIA Mann, Proc. Bost. Soc. Nat. Hist. 10:312. 1866.—This species is not represented in the Hillebrand Herbarium. A cotype of MANN'S species is in the Gray Herbarium, "no. 559 leg. *Mann*, Kealia, Kauai." The capsule (only very young capsules are attached to the sheet in a separate pocket) is not cuboid, the leaves are long, whorled (in fours), thin papery, yellowish pubescent underneath especially along the midrib and slightly so on the upper surface.

HILLEBRAND'S two varieties β and γ have nothing in common with *P. sapotaefolia* Mann. His var. β is identical with *P. kauaiensis* Mann so far as the leaves are concerned; a single cuboid capsule (detached) is fastened in a paper pocket. In fact, HILLEBRAND'S label has the name first as *P. kauaiensis*, which he crossed out and wrote underneath "*sapotaefolia* fol. oppositis. Mts. of Waimea,

Kauai"; the following legend appears also on the label: "identical with MANN's sp., only leaves not ternate, *Knudsen* 38."

HELLER's *P. cruciata* is identical with *P. kauaiensis* Mann. HELLER's no. 2870, labeled *P. sapotaefolia* var. β Hbd., has nothing to do with the plant of that name. It cannot be determined, however, as the specimen is in neither flower nor fruit.

Of HILLEBRAND's var. (?) γ *procumbens*[1] there are two sheets in the Berlin Herbarium, "leg. *Knudsen* no. 165, high mountains of Waimea." This is not a variety of *P. sapotaefolia*, but a distinct species. The writer, in his book on the *Indigenous trees of the Hawaiian Islands*, expressed a similar view, but could make no definite statement, as he had not seen the Hillebrand nor the Harvard collection. HILLEBRAND's label on the plant collected by *Knudsen* (no. 165) bears the following legend:

> This is probably *P. sapotaefolia;* the leaves agree entirely with *Mann's* no. 557, which is *P. sapotaefolia* fol. opposit., not *P. oblongifolia* as wrongly labeled. It is true that in the specimen there is only one flower in each axil, but on close examination the pedicel is found to rest on a very short peduncle; and in no. 559, the true type of *P. sapotaef.* fol. *3-natis*, there can be distinctly seen, alongside the one developed flower, quite a numerous cluster of small undeveloped buds, so that the inflorescence seems to be considered subumbellately many-flowered.

Portion of HILLEBRAND's specimen leg. *Kn.* no. 165 is in College of Hawaii Herbarium. Of the typical *P. sapotaefolia* H. Mann, the College of Hawaii Herbarium possesses a specimen collected by *Faurie* (*F.* 188), C. H. Herb. no. 12710.

Pelea Gayana, n. sp.—*P. sapotaefolia* Mann var. (?) γ *procumbens* Hbd. Fl. Haw. Isl. 63. 1888.—A small procumbent shrub with terete glabrous branches; leaves opposite, elliptical-oblong, equally acute at both ends, thin chartaceous, glabrous on both sides, 10–13 cm. long, 3.5–4.5 cm. wide, on furrowed petioles 15–20 mm. long, dark green above, pale underneath, the midrib prominent underneath, the lateral veins united by an irregular arched intramarginal nerve; inflorescence in the axils of the leaves, very shortly pedunculate (about 1.5 mm.); pedicels bracteolate in lower and upper third, bracteoles 0.5 mm., pedicels filiform, 8 mm.

[1] Flora Hawaiian Islands, 63. 1888.

FIG. 1.—*Pelea Gayana* Rock; type no. 1972

when in flower, 25 mm. with fruit; flowers very small, sepals broadly ovate, acute, about 1 mm., puberulous; petals ovate, acute, 2.5 mm.; stamens about one-third the length of the petals, all of equal size; ovary deeply lobed, puberulous; capsule puberulous, thin papery, only one locule usually maturing, often with one or two abortive ones, locules divided almost to the base but still united; seeds not seen.

KAUAI.—Swampy forest on the high plateau of Waimea, elevation 4500 ft., collected in company with Mr. FRANCIS GAY of Kauai, who knew the plant by its native name "Kaleiohiiaka"; fruiting March 3, 1909, *Rock*, type no. 1972 in College of Hawaii Herbarium; flowering September 1909, same locality, *Rock* no. 5285 in College of Hawaii Herbarium.

HILLEBRAND'S specimen in the Berlin Museum, *Knudsen* no. 165, belongs here; a portion of this specimen is deposited also in the College of Hawaii Herbarium.

PELEA CINEREA (Gray) Hbd. var. **rubra,** n. var.—*P. oblongifolia* Gray β var. (?) Hbd. Fl. Haw. Isl. 65. 1888; *P. cinerea* (Gray) Hbd. var. δ Rock, not Hbd. in Indig. Trees Haw. Isl. 239. 1913.—Shrub with rambling branches; leaves elliptical to elliptical-oblong, thick chartaceous, glabrous on both sides, dull green, acute at apex, mucronate, rounded at base or subcordate, 7.5–9 cm. long, 3–4.5 cm. wide, on petioles 1.5 cm. long; peduncle 3 mm., stout and quadrangular; the single hirsute pedicel 2 mm.; flowers unknown; capsule hirsute with reddish hair, the cocci (separated) divided to the base, cohering only at the very base, 1.5 cm. long, nearly 1 cm. high, strongly nerved, endocarp hirsute, pale yellowish, and free.

HAWAII.—Lava beds of Huehue, North Kona, fruiting June 6, 1909, *Rock* no. 3565 type in College of Hawaii Herbarium.

This variety of *P. cinerea* was doubtfully referred to *P. oblongifolia* by HILLEBRAND, who collected it in South Kona, Hawaii. Of his fruiting specimen in the Berlin Herbarium only one coccus of each of the two capsules is developed, the others are abortive. This might have misled him, as it cannot be determined clearly whether the cocci are cohering or not. In the writer's specimen, which is identical with that of HILLEBRAND, the carpels are discrete and therefore must be referred to *P. cinerea* (Gray) Hbd. The writer had previously referred it to HILLEBRAND'S var. δ of that species. It is apparently intermediate between *P. cinerea* and *P. elliptica*.

PELEA CINEREA (Gray) Hbd. var. SULFUREA Rock.—This is HILLEBRAND'S β, of which there is only one sheet in the Berlin Herbarium collected on Lanai. No specimen is represented from Maui. The writer collected this variety on the Island of Maui above Makawao slopes of Mount Haleakala. The leaves are pale and more or less glabrous on both sides. The capsule is smaller and sulphur-yellow. HILLEBRAND'S Lanai specimen has darker leaves, with a dirty olivaceous tomentum. A portion of his specimen is in the College of Hawaii Herbarium, also *Rock* no. 8550, from Maui.

PELEA CINEREA (Gray) Hbd. var. HAWAIIENSIS (Wawra) Rock.—*P. hawaiiensis* Wawra, Flora 110. 1973; *P. cinerea* (Gray) Hbd. var. γ Hbd. Flora Haw. Isl. 69. 1888.—Of HILLEBRAND'S specimens (three sheets in Mus. Bot. Berlin) two were collected by him in 1862 at Kawaihaeiuka on Hawaii, the third is from the Kohala chain, Hawaii. A specimen from Kawaihaeiuka ex. herb. Hillebrand is in the College of Hawaii Herbarium, with specimens collected by the writer in South Kona, Hawaii, on Puuwaawaa Hill, June 15, 1909, *Rock* no. 3654.

The writer's no. 10210 belongs here, although the leaves are glabrate or only slightly pubescent, but are of thick leathery texture as in var. *sulfurea*. They were collected in the Kipuka Puaulu near Kilauea on the slopes of Mauna Loa, alt. 4000 ft. July 1911.

PELEA WAWRAEANA Rock, Indig. Trees Haw. Isl. 231. 1913.—This species, while distinct, is closely related to *P. sandwicensis* Gray. In the Gray Herbarium there is a specimen ex. herb. Hillebrand labeled *P. sandwicensis* Gray *microcarpa*, which is identical with *P. Wawraeana*. It was evidently included by HILLEBRAND in *P. sandwicensis*, as he makes no mention of it in his *Flora;* the locality is given as the western end of Oahu. It is the writer's no. 3020 in the College of Hawaii Herbarium.

In the HILLEBRAND collection his var. β of *P. sandwicensis* is marked as var. *macrocarpa* Hbd., and his var. γ of the same species var. *tenuifolia* Hbd.

In the typical *P. sandwicensis* the capsule has the carpels parted half way and in some specimens even more, while *P. Wawraeana* has distinctly cuboid capsules, which are much smaller than in *P. sandwicensis*.

HILLEBRAND'S var. γ *tenuifolia* of *P. sandwicensis* has also a cuboid capsule, but leaves are three in whorl. He says: "otherwise the same as β." This is not so, for *P. sandwicensis macrocarpa* has larger capsules and the carpels are divided to the middle.

PELEA KNUDSENII Hbd. Fl. Haw. Isl. 70. 1888.—In the Berlin Herbarium is only one sheet of this species, but labeled in Hillebrand's handwriting "*Pelea villosa* Hbd. Waimea, Kauai, *Knudsen* no. 210." It is identical with, and answers the description of, *P. Knudsenii*, which is *Knudsen* no. 210. The writer's *P. multiflora* is probably identical with it, but owing to the much larger inflorescence and numerous flowers, often more than 200 on a single inflorescence, it may be reduced to varietal rank as *P. Knudsenii* var. *multiflora* Rock.

The species occurs on the Island of Kauai, while the variety grows on the southern slopes of Mount Haleakala on the Island of Maui.

PLATYDESMA.—In the Gray Herbarium is a leaf mounted and labeled *Melicope grandiflora* U.S. Expl. Exped. Sandw. Isl. The leaf is recognizable at a glance as belonging to the genus *Platydesma;* it belongs unquestionably to *P. campanulatum* Mann. *P. cornutum* Hbd. occurs only on Oahu, while the former species is found on Kauai, Maui, Hawaii, and Oahu. The specific name given by GRAY is *grandiflora* in the manuscript and *grandifolia* in the publication.[2] Another sheet in the Gray Herbarium contains a paper pocket with a fruit and fragments of fruit identical with HILLEBRAND'S *P. cornutum*. The fragments and fruit were communicated to GRAY by Dr. WM. T. BRIGHAM, of Honolulu, with the remark "Sandwich Islands, sem. in loculis 6" (evidently referring to the number of seeds in each locule). It bears the name of *Melicope* (?) *grandiflora* Gray in GRAY'S handwriting. He evidently associated the fruit collected by BRIGHAM with the leaf shoot collected by the United States Exploring Expedition. A careful illustration of a flower and fruit of what is HILLEBRAND'S *P. cornutum* accompanies the specimen.

PELEA AURICULAEFOLIA A. Gray, Bot. U.S. Expl. Exped. 343. *pl. 36.* 1854.—No specimen exists of this species in the Gray Her-

[2] U.S. Expl. Exped. **14**: 354. 1854.

barium. HILLEBRAND's single specimen in the Berlin Herbarium marked *Platydesma auriculaefolia* (Gray) Hbd. is certainly not a *Pelea* but a *Platydesma*. The leaves in the specimen are opposite and not ternate, and are somewhat auriculate. It is neither in flower nor in fruit. This plant of HILLEBRAND's is identical with the writer's var. *sessilifolium* of *Platydesma campanulatum* collected in the Kohala Mountains on Hawaii, from whence HILLEBRAND's specimen originates. *Platydesma auriculaefolia* Hbd. is not a synonym of *Pelea auriculaefolia* Gray, but a synonym of *Platydesma campanulatum sessilifolium* Rock. The plant represented on the excellent plate in the atlas of the United States Exploring Expedition is a typical *Pelea*.

PELEA GAYANA and P. CINEREA var. RUBRA.

Pelea recurvata, n. sp.—*P. kauaiensis* Hbd. (not H. Mann), Fl. Haw. Isl. 64. 1888.—A small tree 5 m. high with rambling branches (teste HILLEBRAND); leaves opposite, ovate or elliptico-oblong, 10–12.5 cm. long, 5–6.5 cm. wide, on petioles 1.75–2.5 cm. long, moderately acuminate, chartaceous, marginal nerve remote from the edge, with one or two sets of meshes between, shining above, clothed underneath, especially along the midrib, with a dense velvety or cobwebby villosity; flowers small, one or more in a cluster, on filiform pedicels 4–6 mm. long, which are bracteolate at the base; sepals ovate, 2–3 mm. long; petals thin, 3–5 mm. long; capsule thin, deeply 4-parted to near the base, the narrow elongate cocci divaricate and strongly recurved, about 12 mm. long, 4 mm. broad, keeled at the upper suture, one or more often abortive.

KAUAI.—Waimea at elevations of 2000–3000 ft.; *Knudsen* no. 64 in Herb. Hillebrand Berlin Bot. Museum is the type, and part of the type is in College of Hawaii Herbarium no. 12711.

COLLEGE OF HAWAII
HONOLULU

SECRETORY CANALS OF RHUS DIVERSILOBA

JAMES B. MCNAIR

In *Rhus diversiloba* T. and G. the resin passages are situated in the roots, stems, leaves, and fruit in the phloem of the primary vascular bundles. In addition, there are others in the secondary bast of the stem and root.

The root contains a single wide resin canal in each of the phloem portions of the primary bast. In the secondary bast, resin canals in concentric circles with smaller lumina are successively added. After the secondary phloem is formed in the root, the xylem and phloem are formed exactly as in the stem.

In the stem the phloem portion of the primary bundles is separated from the parenchymatous outer cortex by a strong bundle of sclerenchymatous (bast) fibers of crescent-shaped transverse section. These fibrous bundles are almost in contact with one another at their margins, and thus constitute a ring around the outer cortex. Outside of this sclerenchymatic ring no resin passages are found, but large ones are located immediately within it, one in the phloem of each vascular bundle. In the secondary cortex, which is formed later internally, new canals are formed successively in the strands of the bast. The cortical passages of the secondary bast are connected in the internodes by more or less numerous tangential anastomoses, and thus combine to form a more or less complete cylindrical network in the bark concentric with the stem cylinder. The cortical passages in the nodes anastomose with one another. The leaf passages extend up the internode to the plexus of anastomoses.

The vascular bundles which pass into the petiole are arranged in curves to follow the outline of the petiole in its transverse section. These branch when they reach the leaflets. The resin passages are arranged in the petiole as in the primary vascular bundles. The canals may be absent in the weaker bundles, however.

In the midrib of the leaflets the fibrovascular system is divided into two parts. One, the superior, the ventral, is formed of 3

reunited bundles placed under the endophloem; the other, the dorsal, has 5–7 bundles arranged in an arc, and has also 5–7 resin passages in the phloem parts.

All lateral ribs contain at least one passage on their dorsal sides, which is in the phloem as usual. Some of the resin canals seem to end blindly in the spongy parenchyma and palisade parenchyma, while others apparently anastomose in a reticulate manner like the vascular bundles which they accompany.

TRECUL (**7**) noticed in *Rhus Toxicodendron* L., to which *R. diversiloba* is very closely allied, the obstruction of the resin canals at the base of the petiole just before the fall of the leaves. This obstruction is effected by an increase in the parietal cells of the canals, and thus constitutes an instance of tylosis, similar perhaps to the obliteration of the old canals in the bark. The enlarged cells divide and the new ones produce more of the same kind. Soon the ducts are seen on the outside of the parenchyma at the place of insertion of the leaves. At a small distance away in the leaflet the passages have a normal appearance and are filled with sap.

Resin passages in *R. diversiloba* are found also in the mesocarp of the fruit and in the hypocotyl and cotyledons of the embryo, likewise in the phloem. It is interesting to notice how early in the life of the plant these organs of secretion are found, and yet they are confined from first to last in the phloem group.

According to SIECK (**5**), the resin canals of the Anacardiaceae are of schizolysigenous origin.[1] The first development of the intercellular cavities can readily be observed in *R. diversiloba*, which has good clear channels. In the beginning the evolution of the resin tube in this plant is clearly schizogenous. It forms itself from a little group of cells individually much narrower than the other parenchyma cells. A short slit soon appears toward the center of the group. When this slit enlarges itself, a little of the resinous sap appears. The opening, first irregular in outline, enlarges to a channel of considerable size with a regular circular outline and is bordered by narrow cells. This is by far the form most commonly

[1] It should be stated that SIECK worked with *Anacardium occidentale*, which is not very closely related to *Rhus diversiloba*, a fact which may explain the apparent difference in origin of the secretory canals.

noticed and is plainly schizogenous. Some of the secreting cells may eventually break down altogether, to leave their secretions in the cavity formed by their disintegration and thus be designated lysigenous in character. Cavities so appearing in my investigations of this plant may have been due to imperfect sections. At any rate, lysigenous cavities are apparently in the minority.

If these observations be compared with previous works on other Anacardiaceae, it will be seen that there are no essential differences in the arrangement of the intercellular secretory reservoirs. Which genera should be poisonous, or why their poisons should vary, either in physiological action or in chemical composition, cannot be deduced from this part of their anatomies.

Plants other than the Anacardiaceae that secrete resin, emulsions of gum-resin, etc., in passages are as follows: Coniferae, Alismaceae, Aroideae, the tubifloral Compositae, Umbelliferae, Araliaceae, Pittosporeae, many species of *Mamillaria*, Clusiaceae, and *Ailantus* and Bruceae of the Simarubeae.

The abundance and comparatively large size of the resin ducts, together with their fusing, make an intercommunicating system. When a wound is made, the sap and its poison are quickly pressed out, either by the tension of the elastic walls of its own cells or by a combination of both. In the spring the sap is very watery, while the autumn product is much thicker, granulous, and slower in exudation. The sap, which is properly an emulsion, is, when first expressed, white or light gray in color, and as it quickly coagulates and browns in the air, it forms an efficient covering for the wound. The sap is darkened in the air mainly by oxidation, as has been shown in a former paper (**3**): first, when deprived of oxygen the sap darkens but very slowly; secondly, when in the presence of oxygen the sap darkens rapidly; and finally, ultimate chemical analyses of the sap before and after darkening show an appreciable difference only in the oxygen content.

Under the microscope the freshly exuded sap is in part a colorless liquid and in part made up of minute globules. Very soon some of these globules become dark brown, while the fewer remaining globules continue to be colorless. While this change has been taking place, oblong rectangular colorless crystals separate out. The first crystals to separate are larger than those which form

later. This process of crystallization probably has its cause in the evaporation of the menstrum. If these crystals be viewed through a petrographic microscope, they are seen to be birefringent, similar perhaps to those noticed by WIESNER (**8**) in the sap of *R. vernicifera*. On adding water the light colored globules disappear, but the brown ones remain. The addition of alcohol, on the other hand, causes the solution of the brown globules.

The freshly exuded resinous sap of *R. diversiloba* has been shown to be the only part of the plant capable of producing dermatitis (**2**). Consequently those portions of the plant that do not contain the resin ducts do not have this kind of toxic effect. The non-toxic portions are the anthers, pollen, xylem, trichomes, epidermis, and cork cells. The poison has also been shown to be non-volatile, although it may be carried by the particles of soot in smoke.

INUI (**1**) has noticed that the amount of secretion of *R. vernicifera* is influenced by the conditions of light and atmospheric humidity. In potted plants the secretion lessened when carbon assimilation was hindered. Similarly secretion was greater in damp than in dry air. This secretion therefore seems to bear a relation to transpiration and hence to turgor. As the degree of turgor varies indirectly with the amount of transpiration, other things being equal, secretion would be least when transpiration is greatest. Turgor, too, is a necessary accompaniment of growth; flaccid tissues do not grow larger. If those influences which affect *R. vernicifera* have a similar action on *R. diversiloba*, then secretion, and consequently the plant conditions for poisoning, would be greatest during that time of the year when the growth of the plant is most active and the tissues least resistant, in the spring. Obviously enough, when the plant is in full leaf and when growth has diminished, its resistance to injury will be greater and its liability of poisoning less.

In autumn the charming appearance of the luxuriant foliage, when it turns to many shades of scarlet and bronze, speaks a flagrant warning to its victims and is only especially alluring to the unsuspecting. Nevertheless, either the amount or the virulence of the poison in the autumn leaves is less than that of the normal mature leaves (**3**). Of the autumnal leaves the red are less toxic than the yellow, and when the leaves have finally withered and

fallen they are non-toxic. During that period of the year when the plant is leafless the risk of its producing poisoning is least.

This theoretical consideration of the liability of *Rhus* poisoning from a botanical point of view has its counterpart in clinical statistics. The latter lend analogous evidence to the conclusion that spring has the greatest number of cases (see frequency polygons) (**9**).

The number of cases of dermatitis from *R. diversiloba* is influenced, not only by the condition of the plant, but also by those conditions which tend to make individuals come in contact with it or with substances coated with its poisonous sap. ROBERT LOUIS STEVENSON (**6**) describes a tramp in California woods as follows:

> We struggled toughly upward, canted to and fro by the roughness of the trail, and continually switched across the face by sprays of leaf or blossom. The last is no inconvenience at home; but here in California it is a matter of some moment. For in all woods and by every wayside there prospers an abominable shrub or weed, called poison-oak (*Rhus diversiloba*).

Many low plants seek the shelter of the *Rhus diversiloba* shrubs, and some of our loveliest flowers, such as Clarkias, Godetias, Collinsias, Brodiaeas, and Larkspurs, seem to realize that immunity from human marauders is to be had within its safe retreat. JOHN MUIR (**4**) "oftentimes found a curious twining lily (*Stropholirion californicum*) climbing its branches, showing no fear but rather congenial companionship." The desire to gather spring wild flowers is often greater than the fear of *Rhus diversiloba*. Circumstances thus combine to bring victim and culprit together at the time when the culprit is capable of doing the most harm. It may truthfully be said in regard to this poisonous plant, as is said of the Scotch thistle, "no man provokes it without fear of punishment."

Summary

1. The intercellular secretory canals of *Rhus diversiloba* T. and G. are found in the roots, stem, leaves, and fruit in the phloem of the primary vascular bundles. There are other secretory canals situated in the secondary bast of the stem. They are found also in the phloem of the mesocarp of the fruit and in the hypocotyl and cotyledons of the embryo.

2. Their formation may possibly be schizolysigenous. In the beginning they are clearly schizogenous.

3. There are no essential differences in the arrangement of the intercellular secretory reservoirs between the poisonous and non-poisonous Anacardiaceae.

4. From an anatomical standpoint there is no reason why the poisons of the Anacardiaceae should vary either in physiological action or in chemical composition.

5. The fresh sap emulsion is the only part of the plant capable of producing dermatitis.

6. Those portions of the plant that do not contain the resin ducts do not normally have this kind of toxic effect.

7. The non-toxic portions are the anthers, pollen, xylem, epidermis, cork cells, and trichomes.

8. The liability of poisoning from *R. diversiloba* tissues decreases as follows: immature leaves and flower parts (except anthers and pollen), mature leaves, green stems, young roots, woody stems, and woody roots.

9. The liability of poisoning from *R. diversiloba* is greatest in the spring, less in the summer and fall, and least when the plant is leafless.

PASADENA, CAL.

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CURRENT LITERATURE

BOOK REVIEWS

The organism as a whole

The author of this book[1] in his previous writings has concerned himself with particular processes and activities of the organism, but has never given us any adequate consideration of that remarkable order and harmony which make the organism a whole and not merely an aggregate of parts. The title of the book arouses the hope and justifies the expectation that we shall find in it something in the way of a synthesis or some attempt at least to formulate the problem of organic order and harmony in physico-chemical terms. To what extent the book accomplishes this will appear more clearly as we consider its contents.

In the preface the author says, "in this book an attempt is made to show that the unity of the organism is due to the fact that the egg (or rather its cytoplasm) is the future embryo, upon which the Mendelian factors in the chromosomes can impress only individual characteristics, probably by giving rise to special hormones and enzymes." Apparently this conception of the egg cytoplasm and chromosomes is the chief thesis of the book, for it is stated repeatedly in almost the same words. By way of proof, some well known cases of visible cytoplasmic differentiation in animal eggs are cited and their apparent relation to the future embryo is pointed out, but as regards the action of the Mendelian factors the reviewer has not been able to find anything except surmises, suggestions, and opinions, and these do not carry us beyond the original statement. Moreover, no attempt is made to show how the unity of the organism results from this situation in the egg or how the situation itself arises. As LOEB states it, the case looks amazingly like one of pre-established harmony. The cytoplasmic differentiations are there and the Mendelian factors are there, apparently without any previous relation to each other, and it does not appear how they have come to be there. It is difficult to discover where the unity lies.

The second thesis of the book seems to be that the existence of purposeful and harmonious organisms is explicable in mechanistic terms on the basis of evolutionary theory, provided we substitute the De Vriesian for the Darwinian conception. In support of this thesis the stock arguments are presented: (1) that mutations are inherited, while fluctuating variations are not; and

[1] LOEB, JACQUES, The organism as a whole from a physico-chemical viewpoint. pp. viii+379. New York: Putnam Sons. 1916.

(2) that organisms which are not purposeful and harmonious cannot persist. We look in vain for any consideration of the organism as a whole, that is, of the nature of its wholeness. There is no discussion of the morphological problem, but structure is simply accepted or assumed as required, and the author is chiefly concerned with certain chemical aspects of life.

If, however, the book is not exactly what its title leads us to expect, it nevertheless contains a great variety of facts, suggestions, and hypotheses concerning many aspects of biology, and these are all presented in the author's usual interesting and persuasive style. It is quite impossible even to mention all the various fields which the author enters, but a brief survey of chapters will indicate the range of the book.

In an introductory chapter CLAUDE BERNARD'S "design," DRIESCH'S "entelechy," and VON UEXKÜLL'S "supergenes" are briefly considered and discarded as superfluous.

The contents of the second chapter are indicated by its title: "The specific difference between living and dead matter and the question of the origin of life." LOEB refutes very effectively the argument for a fundamental similarity between organisms and crystals. The organism differs from the crystal and other inorganic systems in that it synthesizes its own specific substance out of non-specific materials. He then argues for the immortality of the body cell, but without discussion of the phenomena of senescence, and finally reaches the conclusion that life is either eternal or that there must be synthetic enzymes which form molecules of themselves from a nutritive solution. Apparently he fails to see that such enzymes offer no solution of the problem of the origin of life, for, according to his own definition of living things, these enzymes must themselves be alive.

The third chapter, "The chemical basis of genus and species," discusses specificity in grafting, blood and serum specificity, etc., and concludes that the basis of specificity is in the proteins. The next two chapters, "Specificity in fertilization" and "Artificial parthenogenesis," are in large measure an account of the work of LOEB and his students, and contain little of importance that has not already appeared in the author's earlier books. Recent work on the problem by F. R. and R. S. LILLIE and others is briefly mentioned, but the author's conclusions remain essentially unaltered.

The sixth chapter, "Determinism in the formation of an organism from an egg," is an argument in support of the view that the egg cytoplasm is the embryo in the rough. The cases of visible cytoplasmic differentiation in animal eggs and its apparent relation to later development are cited, but no mention is made of the centrifuge experiments which demonstrated that, in most cases at least, this visible differentiation is not an essential feature in further development. After some consideration of the development of isolated blastomeres, LOEB concludes that the only regulation in the egg consists in a flow of materials, but he neglects to account for the remarkably orderly character of the flow.

Following is a chapter on "Regeneration," which begins with a statement of SACH's theory of formative substances. The reviewer finds much to criticize in this chapter, since his own work in this field has led him to very different conclusions from those reached by LOEB, but only a few points of more general interest need be noted here. Special substances are postulated to account for all phenomena of regeneration, there is no adequate discussion of nor even reference to other hypotheses, and most of the experiments cited are those of LOEB and his students. In the discussion of regeneration in plants only the author's experiments on *Bryophyllum* are mentioned. One would never even suspect from reading the book that the problem of regeneration or experimental reproduction had ever received any attention from the botanists. MCCALLUM's work is completely ignored. In the case of *Bryophyllum*, which is discussed at some length, LOEB's argument is briefly this: certain substances determine the growth of a particular organ, for example, a growing tip, and the growing organ attracts these substances. In other words, the substances are necessary to make the organ grow, while on the other hand, it must begin to grow in order to obtain these substances. These substances are assumed to be in the fluids of the body and to be carried by these except in so far as they are "attracted" by particular growing tips. If this is the case, how is it possible that one growing tip can prevent another, perhaps in its immediate vicinity, from obtaining *any* of the substance necessary for its growth? But this is what LOEB assumes and asks us to believe.

In discussing certain experiments on *Planaria*, BARDEEN's earlier conclusions are accepted and no mention is made of the fact that BARDEEN himself showed in later work that they were incorrect, and that more recent work has still further demonstrated that the factors concerned are very different from those which LOEB postulates. The author's experiments, made some 25 years ago, on the effect of gravity in determining the polarity of the hydroid *Antennularia* are described, but there is no discussion or even mention of the fact that other investigators have been quite unable to confirm them.

The flow of substances, assumed by LOEB to occur in pieces of the stem of the hydroid *Tubularia* toward one pole or the other as the facts of regeneration demand, is entirely without any basis of evidence, and the simultaneous regeneration of hydranths or partial hydranths at both ends of a short piece with no stem between them presents difficulties to this interpretation. Since the short piece produces hydranths and these hydranths occupy its whole length, it must have contained enough of the formative substances to produce them. If this is the case, why is any flow from other parts necessary for the production of a hydranth in longer pieces, as the hydranth-forming region must have enough of it to develop a hydranth? Moreover, if a short piece of the stem can transform itself completely into one or more hydranths or partial hydranths without the presence of other parts, how can the development of the hydranth be determined by the influence of other parts, as LOEB maintains? Further criticisms of this chapter might be made, but perhaps

these are sufficient to show that LOEB's interpretations throw no light on the problem.

Chapter VIII, "Determination of sex, secondary sexual characters, and sexual instincts," deals first with the cytological basis of sex-determination. LOEB accepts in their most extreme form the conclusions of the cytologists concerning the "sex-chromosomes," and says that "thus far all the facts agree with the dominating influence of certain chromosomes upon sex-determination." Actually, however, these facts, assuming that they are all facts, have been interpreted very differently by different authors. Sex-determination in plants is mentioned in only two brief sentences. The discussion of the physiological basis of sex-determination is largely concerned with sex-hormones, experimental and parasitic castration, and the influence of nutrition on sex. The intersexual forms of the moth *Lymantria* obtained by GOLDSCHMIDT are described, but without comment.

The account of "Mendelian heredity and its mechanism" in chapter IX begins with a brief outline of Mendelian theory and of MORGAN's hypothesis of localization of the Mendelian factors in the chromosome, concluding with the statement "biology has thus reached in the chromosome theory of Mendelian heredity an atomistic conception, according to which independent material determiners for hereditary characters exist in a linear arrangement in the chromosome." The author then inquires "what makes a harmonious organism out of this kaleidoscopic assortment?" The answer is that the egg cytoplasm is the embryo in the rough, and that each determiner in the chromosomes gives rise to one or more substances which influence various parts of the body. But when we ask how the egg cytoplasm comes to be the embryo, and in the rough, and how it happens that the substances produced are adjusted to the different regions of the cytoplasm, we find no answer except the assertion that evolution can produce harmonious organisms, because those that are not harmonious are eliminated.

Chapter X on "Animal instincts and tropisms" adds nothing essential to LOEB's previous discussion of the subject, and is open to the same criticisms. The chapter is devoted largely to the consideration of reactions to light and the attempt to show that they are in accord with the Bunsen-Roscoe law of photochemical reactions, according to which the chemical effect is within certain limits equal to the product of intensity into duration of illumination. There is but little discussion of fact or theory which does not agree with LOEB's conclusions. As regards the trial and error theory, LOEB says that it has been refuted by practically all workers in the field. Students of animal behavior will be interested to discover that the question has been settled.

"The influence of environment," chapter XI, is devoted largely to consideration of the influence of temperature, the temperature coefficient of physiological processes, salt antagonisms, and balanced solutions. This is followed by a chapter on "Adaptation to environment," which is somewhat less extreme than some of the author's earlier discussions of the subject, but

in which his skepticism as to the occurrence of adaptation is clearly evident. LOEB seems to believe that if a case of apparent adaptation can be stated in terms of the action of particular substances on particular parts or stages, it is thereby removed from the category of adaptation. Actually of course this line of reasoning does not touch the real problem, for the harmonious relations between substance and organ of apparent specificity, time, or intensity of action, may themselves be adaptations. A chapter on "Evolution," consisting of three pages, is little more than an acceptance of the De Vriesian as opposed to the Darwinian conception of the mechanism of evolution.

The final chapter, "Death and dissolution of the organism," begins with an interesting consideration of autolysis and its relation to the cessation of oxidations, lack of oxygen, and change in hydrogen ion concentration. Death in the higher animals, he says, is due to cessation of oxidations. The statement "it is an unquestionable fact that each form has a quite definite duration of life" is not in agreement with recent experimental work on some of the lower animals, and to say that "no species can exist unless the natural life of its individuals outlasts the period of sexual maturity" is to ignore the fact that various forms, not only among the protozoa which LOEB regards as immortal, exist for many generations, probably indefinitely, with only agamic reproduction. Are such forms also immortal? As regards the protozoa, however, he fails to note that the "immortality" depends upon reproduction. Any protoplasm concerned in reproduction is just as immortal as protozoan protoplasm. This sort of immortality depends upon the processes of rejuvenescence associated with reproduction, and is merely the continuity of life through the reproductive process. As might be expected from the suggestion in chapter II that the body cell is immortal, LOEB agrees with METCHNIKOFF in regarding senescence and death as essentially an accident due to the formation in the body of poisons through bacterial action or otherwise. Special chemical substances are the cause of death as well as of most of the phenomena of life.

This then is apparently LOEB's conception of the organism as a whole, a "kaleidoscopic assortment" of material factors or determiners located in the chromosomes, producing substances which act on another assortment of materials in the cytoplasm. In chapter II he says "biology will be scientific only to the extent that it succeeds in reducing life phenomena to quantitative laws." Nevertheless, his interpretations are predominantly qualitative, and in various cases he has ignored quantitative interpretations offered by others. We find, for example, no mention even by way of refutation of RIDDLE's quantitative hypothesis of sex. The evidence in favor of a quantitative conception of polarity and of initiation of differentiation is not considered, and no mention is made of the quantitative hypotheses of senescence, which, by the way, can be interpreted in terms which are completely in accord with the autocatalytic theory of growth in favor of which LOEB has repeatedly declared

himself. There seems to be a certain inconsistency in this preference for qualitative interpretations. If scientific biology is essentially quantitative, as LOEB maintains, we have the right to demand adequate grounds for his rejection or failure to discuss quantitative as opposed to qualitative interpretations.

Few biologists of the present day will deny the importance of chemical or transportative correlation, that is, the production, transportation, and action in the organism of chemical substances, many of which are supposed to be specific. There is, however, another sort of physiological correlation, namely, transmissive or conductive correlation, which finds its highest development in the nervous system. In this sort of correlation the essential feature is the transmission of energy rather than the transportation of materials. There can be no doubt that in organisms which possess a differentiated nervous system this is the chief factor in maintaining the integration of the organism as a harmonious whole. But biologists are very generally agreed that the nervous system adds nothing new to the organism, for transmissive correlation exists even where there is no visibly differentiated nervous system. In fact, the nervous system is the structural and functional expression of transmissive relations between parts which exist both embryologically and phylogenetically before its development. Unless we assume the existence of an entelechy or supergenes or some other non-mechanistic ordering and controlling principle, we cannot escape the conclusion that the starting-point of physiological integration is to be found in the initiation and transmission from one part to another of dynamic changes, not of material substances.

In a discussion of the organism as a whole we should expect to find something concerning the nervous system, and how it has become of such importance in physiological integration. LOEB, however, merely refers in the preface to his "comparative physiology of the brain" as supplementing the present book. The German edition of that work appeared in 1899. It seems to many of us that after 18 years there might at least be something to add to the original discussion, particularly as regards the integrating function of the nervous system or of protoplasmic conduction in general. Apparently, however, transmission, conduction, and nervous function possess no fundamental significance for the author in relation to the wholeness of the organism.

The analogy between the biological individual, the organism, and the social organism, the state, has often been noted both by biologists and sociologists. The reviewer believes that there is more than an analogy here. Both the organism and human society represent the reactions of living protoplasm to its environment, and in the integration of human individuals into an orderly and harmonious whole we find a fundamental similarity to the process of physiological integration within the organism. A moment's thought is sufficient to show that in the integration of human beings into an orderly community or state the transmissive relations are the primary factors. The

production and interchange of substances among human beings, which we know as barter and exchange or commerce, can never of itself integrate those concerned into an orderly and harmonious whole, a tribe or nation. Government of some sort, that is, authority and its transmission, is the real integrating factor, and commercial relations do not assume an orderly harmonious character until at least some degree of integration has taken place.

LOEB is attempting to conceive the organism as a whole in terms of the commercial relations between its parts. This is as if one should attempt to interpret a nation or state and its origin in terms of the production and exchange of commodities between its constituent members or groups. The one attempt is as futile as the other. Actually LOEB has failed to see the organism as a whole because he has been so engrossed with the particular activities of its various parts and their relation to environment. Evidence is rapidly accumulating to show that control, that is, government in the organism, is a physiological fact, and the primary fact in the integration of the individual, that such control originates in quantitative differences in the velocity of metabolic reactions and the associated protoplasmic differences together with the transmission of energy changes resulting from these differences rather than in the transportation of substances, and that the nervous system is morphologically and physiologically merely the expression of the transmissive relations which exist from the beginning of individuation. This conception is not only supported by many lines of evidence, but it comes much nearer LOEB's definition of scientific biology as the reduction of life phenomena to quantitative laws than does his own interpretation in terms of formative or nutritive substances. Certainly the egg is the embryo in the rough, as LOEB maintains, and so is any other reproductive cell or cell mass, but since the embryo and the organism developing from it are orderly and harmonious wholes, the egg and other reproductive bodies must also be wholes of the same sort. It is here that we come face to face with the problem of the organism as a whole, and LOEB offers us nothing but the bare assertion, oft repeated, that the egg is the embryo in the rough, and this is merely the statement of the problem, not the solution. He has contented himself with this mere statement of the real problem and has passed on to devote himself to the innumerable details of the activity of the organism in which the wholeness is already established and effective. If this were all that mechanistic biology has to offer toward the solution of the problem of the organism, the vitalist might rest content.

If we search in vain for the organism as a whole in the book, however, there is nevertheless much of interest. It must be admitted that those familiar with LOEB's earlier books will find little that is new, particularly in certain chapters, and that often there is no consideration of the work of others, but, as a statement of LOEB's conception of the organism, the book cannot fail to interest the biologist, even though, or perhaps because, he will find himself unable to assent to many of its conclusions.—C. M. CHILD.

NOTES FOR STUDENTS

Transpiration studies.—An excellent review of recent investigations on transpiration, by KNIGHT,[2] includes the principal contributions for the five years previous to 1916. Conspicuous among the more recent investigations is that by BRIGGS and SHANTZ[3] upon the comparison of evaporation from various types of atmometers and free water surfaces on shallow and deep tanks, with transpiration from alfalfa (*Medicago sativa*). The departure of the hourly evaporation rate of the porous cup atmometers from the hourly transpiration rate of the alfalfa seems to be due largely (1) to the marked increase in the evaporation over transpiration during the night hours; (2) to the more marked response of the atmometers to changes in wind velocity; and (3) to the lack of proportionate response on the part of the atmometers to changes in solar radiation. The departures amount to 90 per cent for the deep tank, 50 per cent for the white cylindrical atmometer, 40 per cent for the brown cylinder, the white sphere, and the Bellani plate, and 17 per cent for the shallow blackened tank, showing no very close correspondence for any of the systems, but decidedly the best approximation in the last mentioned. In such a tank, 91 cm. in diameter and 2.5 cm. high, the water was automatically maintained at a depth of 1 cm.

In view of the divergence of the evaporation rates from the two tanks employed in these experiments, it becomes evident that THOMAS and FERGUSON[4] have not taken into account all the variables in their effort to obtain a law of evaporation from circular surfaces. This was sought primarily for use in standardizing atmometers and other instruments for comparison of water loss with that from the plant in the process of transpiration. Their conclusion that evaporation from a circular water surface is not proportional to its area was already familiar to us, and has been emphasized not only in the investigation cited but also by Livingston.[5]

To facilitate critical studies of transpiration, BLACKMAN and KNIGHT[6] have devised an apparatus for controlling air movements about plants under investigation and have been able to have constant currents up to a speed of 25 m. per minute. Using this apparatus and otherwise securing carefully

[2] KNIGHT, R. C., Recent work on transpiration. New Phytol. **16**:127–139. 1917.

[3] BRIGGS, L. J., and SHANTZ, H. L., Comparison of the hourly evaporation rate of atmometers and free water surfaces with the transpiration rate of *Medicago sativa*. Jour. Agric. Research **9**:277–292. 1917.

[4] THOMAS, NESTA, and FERGUSON, ALLAN, On the reduction of transpiration observations. Apn. Botany **31**:241–255. 1917.

[5] LIVINGSTON, B. E., Atmometry and the porous cup atmometer. Plant World **18**:51–74. 1915.

[6] BLACKMAN, V. H., and KNIGHT, R. C., A method of controlling the rate of air movement in transpiration experiments. Ann. Botany **31**:217–220. 1917.

controlled conditions, KNIGHT[7] has performed experiments with various plants with results which show no close agreement between stomatal opening and rate of transpiration, but which tend to demonstrate that the water content of the leaf is an important factor in controlling its water loss by transpiration, and further that stomatal aperture is not reduced by slight water deficiency in the leaf, but is very sensitive to light changes. On the whole, his results support LIVINGSTON'S contention of the regulatory importance of "incipient wilting," and are directly opposed to DARWIN'S theory that stomatal aperture plays the primary rôle in the regulation of transpiration.

Working with detatched leaves and with potted plants, MARTIN[8] has confirmed previous conclusions in finding that films of Bordeaux mixture cause decided acceleration in the rates of transpiration, and that their influence is apparent as soon as the spray dries upon the leaves. More recently results of the same nature were obtained by SHIVE and MARTIN,[9] using cobalt chloride paper. The indices of the transpiring power of the sprayed leaves are shown to be rather more than 20 per cent higher than for the untreated leaves of the same plant. It is also interesting to note that the investigators express their confidence in the accuracy of the results obtained by the cobalt chloride method, which may now be regarded as a reliable method especially adapted to field use.

Not only are fungicides instrumental in increasing transpiration, but the fungi themselves may also act in a similar manner, as has been shown by WEAVER[10] for cereal rusts. Here the increase in transpiration occurs about the time the pustules break through the epidermis, and the amount of increase is closely related to the pustular area.

Experimenting upon the relations expressed in the comparison of the relative water loss from the plant and the atmometer, termed by LIVINGSTON "relative transpiration," KNIGHT[11] finds that this does eliminate the influence of changes of temperature and relative humidity on rate of transpiration. He asserts, however, that "relative transpiration" does not necessarily represent changes in the intrinsic transpiring power of a plant unless conditions of air movement are constant. This is because of the unequal response of plant and atmometer to changes in wind velocity.—GEO. D. FULLER.

[7] KNIGHT, R. C., The interrelations of stomatal aperture, leaf water-content, and transpiration rate. Ann. Botany **31**:221–240. 1917.

[8] MARTIN, W. H., Influence of Bordeaux mixture on the rates of transpiration from abscissed leaves and from potted plants. Jour. Agric. Research **7**:529–548. 1916.

[9] SHIVE, J. W., and MARTIN, W. H., The effect of surface films of Bordeaux mixture on the foliar transpiring power in tomato plants. Plant World **20**:67–86. 1917.

[10] WEAVER, J. E., The effect of certain rusts upon the transpiration of their hosts. Minn. Bot. Studies **4**:379–406. 1916.

[11] KNIGHT, R. C., "Relative transpiration" as a measure of the intrinsic transpiring power of the plant. Ann. Botany **31**:351–360. 1917.

Grasslands and forests of Washington.—A recent study by WEAVER[12] of the vegetation of adjacent portions of Washington and Idaho affords an excellent example of modern ecological investigation. After a sketch of the physiography and geology of the region, the results of quantitative studies of the principal physical factors involved are reported. Temperature, rainfall, evaporation, and soil moisture data are given, the last two receiving most emphasis, as they express the important aspects of the water relationship of a vegetation in which the available moisture is undoubtedly the limiting factor. A preliminary report of the evaporation studies was previously made and reviewed in this journal,[13] and the present more complete report only tends to confirm the conclusion that the differences of the rates of evaporation in the various plant communities are sufficient to be important factors in causing succession. The studies of soil moisture also show that this important factor varies in amount directly with the order of the occurrence of the various communities in the order of succession. Incidentally it may be noted that the soil of the *Thuja* association has a very high water holding capacity, showing during the months of July and August a supply of "growth water" of over 40 per cent, thus providing for the development of the very complete mesophytism seen in this climax conifer forest.

The western conifer forests here show a succession from shrub of xerophytic character through *Pinus-Pseudotsuga*, *Larix-Abies* associations to the luxuriant conifer forest composed almost exclusively of *Thuja plicata*. The secondary species of this forest are carefully considered, as well as the reforestation of cutover areas and burns.

The scrub formation dominated by *Artemisia tridentata* and the hydrarch succession from ponds and streams are described, but perhaps aside from the forest the most important and interesting community is the grassland termed "prairie-plains formation" and dominated by *Agropyron spicatum* and *Festuca ovina*. It presents seasonal aspects varying from rich grassy verdure during the comparatively moist spring and early summer, to the sere brown of the arid late summer. The soil moisture determinations show the gradual depletion of growth water from the surface stratum, where it exists in June to the depth of 5 ft., by the middle of August. The response to this distribution of moisture is seen in the luxuriant spring growth and early flowering of the comparatively shallow rooted grasses which dominate the community, and the entire absence of late blooming grasses. It is also apparent in the development of extensive root systems in such conspicuous herbaceous plants as *Balsamorhiza sagittata*, *Hieracium Scouleri*, and *Lupinus ornatus*. This extensive root development has been carefully studied by the same investigator.[14]

[12] WEAVER, J. E., A study of the root systems of prairie plants of southeastern Washington. Plant World **18**:227–248; 272–292. *figs. 18*. 1915.

[13] BOT. GAZ. **59**:71–72. 1915.

[14] WEAVER, J. E., A study of the vegetation of southeastern Washington and adjacent Idaho. Univ. Neb. Studies **17**:1–114. 1917.

who finds the generalized root type most extensively developed and a penetration of 60–70 inches not uncommon.

The reports abound in interesting details too numerous to mention in a review, are carefully organized and well illustrated with graphs, drawings, and photographs, forming a notable contribution to our knowledge of the vegetation of an unusually interesting region.—GEO. D. FULLER.

Taxonomic notes.—BLAKE[15] has described a new variety of *Vernonia altissima* (*taeniotricha*) which occurs from Indiana and Illinois to Missouri and Mississippi.

BRITTON[16] has published a list of the Cuban species of *Rhynchospora*, with an analytical key. It is in Spanish and appears among the publications entitled "Memorias de la Sociedad Poey." The author lists 55 species, 6 of which are described as new.

BURT,[17] in continuation of his studies of North American Thelephoraceae, has monographed the genus *Coniophora*, recognizing 19 species, 5 of which are described as new.

DAVIE,[18] in connection with the publication of a list of plants collected in Brazil in 1914, has described new species in *Gaultheria* and *Pleurostachys*.

FERNALD,[19] in a series of short papers, has described new species and varieties in *Saxifraga* (province of Quebec) and *Vitis* (New England); also new varieties in various species of *Polygonum*, *Ranunculus* (4), *Anemone*, *Saxifraga*, *Cyperus*, *Stenophyllus*, and *Aster*.

FAWCETT and RENDLE[20] have described 3 new species of *Byrsonima* and a new *Zanthoxylum* from Jamaica.

HILL[21] has published a revision of the genus *Strychnos* in India and throughout the East. In that region he recognizes 91 species, 24 of which are described as new.

HEMSLEY[22] has described a new arborescent genus of Euphorbiaceae (*Riseleya*) from the Seychelles. It seems to be restricted to Mahé, where it was formerly common in the mountains.

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[15] BLAKE, S. F., Rhodora **19**:167. 1917.

[16] BRITTON, N. L., El genero *Rhynchospora* Vahl, en Cuba. Contrib. Jard. Bot. N.Y. no. 194. pp. 16. 1917.

[17] BURT, E. A., The Thelephoraceae of North America. VIII. *Coniophora*. Ann. Mo. Bot. Gard. **4**:237–269. *figs. 19*. 1917.

[18] DAVIE, R. C., Some Brazilian plants. Jour. Botany **55**:215–223. 1917.

[19] FERNALD, M. L., Contrib. Gray Herb. **19**:133–155. 1917.

[20] FAWCETT, W., and RENDLE, A. B., Notes on Jamaica plants. Jour. Botany **55**:268–271. 1917.

[21] HILL, A. W., The genus *Strychnos* in India and the East. Kew Bulletin, 1917: nos. 4 and 5. pp. 121–210.

[22] HEMSLEY, W. B., and TURRILL, W. B., Plants of Seychelles and Aldabra. Jour. Botany **55**:285–288. 1917.

HITCHCOCK and CHASE[23] have published a manual of all the known grasses of the West Indian Islands. The term "West Indies" is defined as including Bermuda, the Bahamas, Trinidad, and Tobago, but excludes the Dutch Islands off the coast of Venezuela. The publication contains descriptions of 455 species, representing 110 genera, including 17 new species and a new genus (*Saugetia*) related to *Gymnopogon*.

STEPHANI[24] has issued the fifth volume of his *Species Hepaticarum*, which deals with the Acrogynae, along with title page and index. He describes 296 species, chiefly established by himself, representing 16 genera, 9 of the species being new. The large genera are *Aneura* (113 spp.) and *Anthoceros* (64 spp.).

WERNHAM,[25] in continuation of his studies of tropical American Rubiaceae, has described 7 new species of *Psychotria*. The same author[26] has described 10 new species of *Palicourea* and 2 new species of *Cephaëlis* from tropical America, chiefly Colombia.—J. M. C.

Sap concentration and plant communities.—Having developed a method of determining the osmotic pressure of cell sap by a depression of the freezing point, HARRIS[27] has proceeded to investigate the tissue fluids of plants typical of the deserts of Jamaica[28] and Arizona,[29] of the mesophytic vegetation of temperate regions, and of the rain forests of Jamaica.[30] Aside from an interesting mass of data regarding the peculiarities of the cell sap of individual species, two generalizations stand out as important contributions to ecological science. They are to the effect that (1) there is a direct relationship between growth forms and sap concentration, as shown in the higher osmotic concentration of

[23] HITCHCOCK, A. S., and CHASE, AGNES, Grasses of the West Indies. Contrib. U.S. Nat. Herb. **18**:261–471. 1917.

[24] STEPHANI, F., *Species Hepaticarum*. Vol. V. Acrogynae (pars quarta). Geneva. 1916.

[25] WERNHAM, H. F., Tropical American Rubiaceae. IX. Jour. Botany **55**:251–254. 1917.

[26] ———, Tropical American Rubiaceae. IX. Jour. Botany **55**:279–285. 1917.

[27] GORTNER, R. A., and HARRIS, J. ARTHUR, Notes on the technique of the determination of the freezing point of vegetable saps. Plant World **17**:49–53. 1914.

[28] HARRIS, J. ARTHUR, and LAWRENCE, J. V., Cryoscopic determinations on the tissue fluids of the plants of the Jamaican coastal deserts. BOT. GAZ. **64**:285–305. 1917.

[29] HARRIS, J. ARTHUR, et al., On the osmotic pressure of the juices of desert plants. Science N.S. **41**:656–658. 1915.

HARRIS, J. ARTHUR, and LAWRENCE, J. V., The cryoscopic constants of expressed vegetable saps as related to local conditions in the Arizona deserts. Physiol. Researches **2**:1–49. 1916.

[30] HARRIS, J. ARTHUR, and LAWRENCE, J. V., The osmotic concentration of the tissue fluids of Jamaican montane rain forest vegetation. Amer. Jour. Bot. **4**:268–298. 1917.

the fluids from the leaves of woody as compared with those from herbaceous plants, and (2) that the sap concentration shows a variation corresponding to the xerophytism of the plant community from which the fluids are obtained.

The importance of the latter relationship has been given emphasis in a paper which gives a summary of results concerning large and widely differing plant formations.[31] Here it is seen that the concentration of the cell sap of the woody plants varies from 11.44 atmospheres for that from the rain forest and 14.4 for that from mesophytic habitats to 24.97–30.05 atmospheres for the fluids of desert plants. Herbaceous plants from these same habitats show sap concentration values of 8.80, 10.41, and 15.15 atmospheres respectively. As might be expected, succulent halophytes show even higher concentrations, culminating, perhaps, in 49.7 atmospheres for *Batis maritima*. Curiously enough, the epiphytes of the rain forest show concentrations of a low order, such as 3.34–4.88 atmospheres for the epiphytic Orchidaceae from Jamaica and Florida.

These and other similar results are sufficient to demonstrate that in this line of investigation there has been found a means of expressing in a quantitative manner the sap properties of both large and small plant communities; hence not only must the results themselves be regarded as important, but a much higher value must be placed upon the introduction of a method which will tend to exactness in studies of the physiological plant geography.—GEO. D. FULLER.

Natal vegetation.—In advancing our acquaintance with the vegetation of South Africa, BEWS[32] has made a study of the species native to Natal according to RAUNKIAER'S life-forms, and has expressed the results in a biological spectrum for that part of South Africa. Some of the conspicuous features of the vegetation as shown by this analysis are the richness, manifest in more than 3000 species, and the small number of large phanerophytes which is far below the average in contrast with the abundance of lianas, chamaephytes, and geophytes. One of the interesting incidental features of the vegetation consists in the presence of stem succulents, all possessing a milky juice, as they belong to the *Asclepiadaceae* and *Euphorbiaceae*.

In a more recent paper, the same writer[33] has described the vegetation of the mountains forming the western boundary of Natal and reaching an altitude of 3400 m. The outline of the plant communities involved shows that grassland and scrub associations predominate. Of the latter, the one developed

[31] HARRIS, J. ARTHUR, Physical chemistry in the service of phytogeography. Science N.S. **46**:25–30. 1917.

[32] BEWS, J. W., The growth forms of Natal plants. Trans. Roy. Soc. S. Africa **5**:605–636. 1916.

[33] ———, The plant ecology of the Drakensberg range. Annals Natal Museum **3**:511–565. 1917.

upon many of the steep slopes is termed "Fynbosch" and described as a sclerophyllous formation comparable to the chaparral of the United States. It is dominated by shrubs with needle and ericoid leaves, conspicuous among which are the genera *Cliffortia* (Rosaceae) and *Erica*, both represented by several species, and a large number of woody Compositae. In its undergrowth, bulbous plants abound. From it BEWS traces a double succession, one to the "bush" or forest, in which *Podocarpus* spp. and *Celtis Kraussiana* are the most abundant trees, the other to the mountain veld. The former is clearly leading to the climax type of tree vegetation developing only under the most favorable conditions of soil and exposure; but the succession in the latter instance does not seem clear, for the veld is apparently more xerophytic, although more extensive than the "Fynbosch."—GEO. D. FULLER.

Germination of tree seeds.—BOERKER[34] has carried on three series of greenhouse cultures to determine the effect of light, soil moisture, and soil texture upon the germination of the seeds of various forest trees. The cultures were extensive and the environmental factors rather carefully controlled. The variations in response are too numerous to be touched upon in a review, but some items of the summary show that it has not been possible to isolate the effect of single factors, as it is stated that shade accelerates germination and this acceleration is due to increase in soil moisture caused by decreased evaporation and transpiration. On the other hand, light is found to play absolutely no part in the germination of tree seeds. Similarly, the differentiation between the effects of soil moisture and soil texture has not been accomplished.

The reaction of different tree species to the different sets of conditions is interesting, and the results should be of practical service to foresters. The increase of length of tap and lateral roots in *Pinus ponderosa* with diminishing soil moisture content may be cited as one of the results. *P. ponderosa* growing in the Rocky Mountains produces smaller seeds that germinate more quickly than those from the same species grown upon the Pacific coast. Similar differences were found for local varieties of *Pseudotsuga taxifolia;* while in both species large seeds proved superior to small, both in higher germination percentage and in the size of the seedlings.—GEO. D. FULLER.

Law of the minimum.—HOOKER[35] gives an interesting discussion on the application of the law of the minimum, or limiting factors, to biological problems. He is perhaps fortunate, in so far as rigid application of the law is concerned, in drawing his early illustrations from simple chemical and physical processes, for it is rapidly becoming a question whether the law applies to plant

[34] BOERKER, R. H., Ecological investigations upon the germination and early growth of forest trees. 8vo. pp. 89. *pls.* 5. Thesis Univ. Nebraska. 1916.

[35] HOOKER, D. H., Liebig's law of the minimum in relation to general biological problems. Science N.S. **46**:197–204. 1917.

activities as generally as or with anything like the rigidity assumed by some workers. The fact of vicarious conditions, or stimuli, renders the conception of limiting factors less definite. In some light requiring seeds, for instance, several things can be substituted for light, as salts, higher temperatures, acids, etc. To speak of the lack of sufficient light as a limiting factor to germination helps little. What should be learned is, what internal condition, or inhibitor, may any one of these factors act upon to initiate growth? The conception of an external condition as a limiting factor frequently leads physiologists to fail to examine the internal mechanism upon which that and other factors play to bring about a given result. The reviewer feels that the law of the minimum should be applied to biological problems with due realization of its limitations. —WM. CROCKER.

Vegetation of Pennsylvania.—A description of the vegetation of the western part of Pennsylvania, by CRIBBS,[36] is organized upon a physiographic basis, including the swamp, lake-forest, ravine-valley, river, and upland series. The plant succession in each series is outlined and the composition of the principal associations indicated. The upland forest serves to indicate the interesting position of the flora, partaking of the northern forms, as seen in *Pinus Strobus*, *Betula lutea*, and *B. lenta*, combined with such typically southern species as *Magnolia acuminata*. The dominant members of the climax forest are found to be *Fagus grandifolia*, *Castanea dentata*, *Quercus alba*, and *Acer rubrum*. With these are associated such others as *Tsuga canadensis*, *Magnolia acuminata*, *Liriodendron Tulipifera*, and *Tilia americana*.—GEO. D. FULLER.

Germination of spores.—BRIERLY[37] has done an interesting piece of work upon spore germination which he summarizes as follows: "The ripe ascospores of *Onygina equina* will germinate directly after a prolonged resting period, which may be curtailed or eliminated by a preliminary treatment of the spores with artificial gastric juice, but not by subjection to low temperatures. The full grown unripe ascospores and the chlamydospores will germinate immediately in the absence of digestive treatment." Demand for a rest period is common in seeds. Frequently the need for a rest period is imposed by the presence of seed coats. Likewise BRIERLY believes this need is imposed in this form by the presence of the spore coat.—WM. CROCKER.

[36] CRIBBS, J. E., Plant associations of western Pennsylvania with special reference to physiographic relationship. Plant World **20**:97–120, 142–157. 1917.

[37] BRIERLY, WILLIAM B., Spore germination in *Onygina equina* Willd. Ann. Botany **31**:127–132. 1917.